

ART. 2. LATE PENNSYLVANIAN AND EARLY PERMIAN VERTEBRATES OF THE PITTSBURGH-WEST VIRGINIA REGION

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INTRODUCTION

The region of the Ohio River drainage in western Pennsylvania, West Virginia and eastern Ohio is unique in America in the presence of an almost unbroken series of essentially continental sediments extending from the typical Carboniferous on into the Permian. There is thus afforded the opportunity of obtaining a sequence of faunas extending on from those of the classical Pennsylvanian to assemblages contemporaneous with the vertebrates of the early Permian Redbeds of the American Southwest. Until recently, little information was available concerning these faunas. A notable advance in our knowledge is afforded through collections made by Carnegie Museum parties in the 1930's. Some account of this work is given in the accompanying geological paper by Mr. William E. Moran and in earlier published notices by the party leader, Mr. John J. Burke (1935, 1937).

If the bulk of the material resulting from these expeditions is compared with that obtainable by an equal amount of labor from, say, the classical Redbeds region of northcentral Texas, one tends, unthinkingly, to be somewhat contemptuous of it. Much consists of isolated and often incomplete vertebral elements, scales and small scraps of sculptured bone—material that a Texas collector would disdain. But, despite the lack of morphological "quality," these specimens are documents of the highest value. The Dunkard material gives us a knowledge of the Permian fauna of a region far removed from the Redbeds regions of the Southwest; the late Pennsylvanian sites, although unfortunately few in number, shed valuable light on the Carboniferous-Permian transition. The collection of these newly assembled materials was a task far harder than that of the Texas "bone-hunter." In the latter semi-arid area, there are extensive fossiliferous exposures of easily worked clays; in the Pittsburgh district, exposures are few and scattered and the main materials are hard limes and "mudstones," worked with the greatest difficulty. Mr. Burke, Mr. Moran and their associates deserve sincere praise for their enthusiasm and persistence in a difficult and discouraging task.

For the most part, the present paper is concerned with the description of this new material collected by the Carnegie Museum explorations of 1934-37. In order to round out our picture of the faunas, however, I have included some account of earlier vertebrate finds from the late Pennsylvanian and Permian of the region and have restudied certain of these materials, particularly the Pitcairn Conemaugh vertebrates in the Carnegie Museum collections, discovered by Raymond and described by Case (1908). I have further included a description of a Dunkard reptile from the collections of the U. S. National Museum. Although the interest of the faunas lies mainly in the reptiles and amphibians present, and to a lesser extent in the freshwater fishes, I have included brief notes on earlier finds of fishes, fresh or salt, from beds of appropriate age in this area. I have not discussed the typical Pennsylvanian faunas of the Allegheny group, but have confined treatment to the Conemaugh and Monongahela groups of the late Pennsylvanian and the Dunkard formations — Washington and Greene — which follow them and close the cycle of deposition in this region.

ACKNOWLEDGEMENTS

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DESCRIPTIONS

Below, I have discussed the material in systematic sequence, beginning with representatives of the "shark" groups, followed in order by

bony fishes, amphibians, reptiles and miscellaneous remains. It must be understood that many of the identifications are tentative and open to doubt because of the fragmentary nature of the material.

Mr. Moran, in his accompanying paper, has listed the various localities visited by the Carnegie Museum parties as a numbered series and has referred alphabetically to localities from which others have obtained tetrapod remains. I have used these numbers and letters throughout and have given more detailed citations only in the case of localities for marine fishes, footprints, etc., with which Moran has not concerned himself. Specimen numbers (unless otherwise specified) refer to the catalogue of vertebrate fossils in the Carnegie Museum.

Acanthodes cf. marshi

At locality 26 several spines were found, flattened ovate in section, with one or both marginal areas thinned and set off from the main portion (no. 8529). These appear to be acanthodian in nature (cf. Watson 1937, pl. 13) and presumably belong to the typically Permian genus *Acanthodes* [*Acanthoessus*]. This is the first identification of an acanthodian in the American Permian and, except for the Upper Pennsylvanian of Mazon Creek, the only identified find of any acanthodian in this continent later than the Devonian. There is no feature visible in these spines by which they can be distinguished from *A. marshi* from Mazon Creek (Eastman 1902: 93-94, pls. 6, 7).¹

Cladodus occidentalis

Raymond (1910: 156) reports this marine shark tooth type from the Ames limestone of the Conemaugh group in the Pittsburgh region. Teeth of this sort are known to occur in a variety of primitive sharks of the cladoselachian and hybodontoid groups, ranging from Upper Devonian to Lower Permian.

Agassizodus variabilis

Raymond (1910: 156) reported teeth of this hybodont shark from the Ames limestone of the Conemaugh group. The present collections contain a tooth of this type from locality 1 (no. 8520) and a damaged tooth (no. 8615), which may be *Agassizodus*, from locality 2 in the Conemaugh group. A fragment of a hybodont spine (no. 8580) from locality 1 may well belong to this genus.

¹ *A. newberryi* from the same locality may well be based on young individuals of *A. marshi*.

Petalodus ohioensis

Teeth of the common marine "pavement tooth" shark genus *Petalodus* are relatively abundant in the marine elements of the Conemaugh. They are reported from the Ames limestone in the Pittsburgh region (Raymond 1910: 148), Athens, Ohio (Condit 1912: 279), and Caldwell, Ohio (Condit 1912: 285); from the Cambridge limestone at Northrup, Ohio (Condit 1912: 273) and Cambridge, Ohio (Safford 1853: 142); the Pine Creek limestone in the Pittsburgh region (Raymond 1910: 156); the Brush Creek limestone at Bens Creek, Pennsylvania (Leidy 1856: 161; 1873: 312, 353; Raymond 1910: 148); the Portersville limestone at Santy, Ohio (Condit 1912: 279). There is little ground for specific determination in this material. Two species of *Petalodus* have been described from the Conemaugh, *P. ohioensis* of Safford (1853: 142) having priority over *P. alleghaniensis* of Leidy (1856: 161).

Fissodus inaequalis

A second petalodont reported by Raymond (1910: 156) from the Ames limestone of the Conemaugh.

Deltodus angularis

A common genus of the bradyodont "shark" family Cochliodontidae, *Deltodus* is reported by Raymond (1910: 156) from the Brush Creek, Pine Creek and Ames limestones of the Conemaugh.

Peripristis semicircularis

A second cochliodont, reported by Condit (1912: 287) from the Ames limestone at New Concord, Ohio.

***Dittodus* sp.**

Under this name may be provisionally ranged the remains, cited below, of freshwater sharks of the type generally known as "pleuracanth"; such remains are common in these collections, as in most continental fossiliferous deposits of late Carboniferous and early Permian ages.

As usual, the most common finds are the characteristic two-pronged teeth usually termed *Diplodus* (preoccupied) or *Dittodus*. Such teeth are found at localities 1, 2, 4, 6, 16, 18, 20, 22, 25, 28, 29, 33, 35 and 37. Two teeth from locality L, tentatively identified by Whipple and Case as belonging to the reptile *Dimetrodon*, appear to be broken prongs of *Dittodus* teeth, of which identifiable specimens are also present in the material. Raymond (1910: 149, 156) notes the presence of "*Dip-*

lodus" teeth in the Birmingham shale and Woods Run beds of the Conemaugh formation in the Pittsburgh region. Price (1927: 228-229, fig. 10, pls. 20, 21; Price, Tucker and Haught 1938: 159) described "*Diplodus*" teeth from the "Round Knob" formation (Pittsburgh shales) of the Morgantown region of West Virginia. Stauffer (1916: 88) cited them from Shadyside, Ohio, in the Lower Washington limestone of the Washington formation; these teeth were formally described by Stauffer and Schroyer in 1920 (p. 147, fig. 40) as *D. washingtonensis*.

It is obvious from the above records that *Dittodus* was present throughout the time of deposition of late Pennsylvanian and early Permian deposits in the Pittsburgh region. Specific identification of isolated teeth is impractical in the present state of knowledge, since there was (as in modern sharks) wide variation in tooth types from one part of the jaws to another.

As in other areas, calcified remains of braincase and visceral arch cartilages are present in the material. Such cartilages are present in localities 1, 6, 20 and 28.

In "pleuracanth," a stout spine, typically with paired rows of denticles, projected from the occipital region of the braincase back over the "neck" region. Such spines are frequently referred to under the generic terms of *Pleuracanthus* (preoccupied), *Xenacanthus* and *Orthacanthus*. These spine types, with well-developed "tooth" rows extending well down the length of the spine, are found in various Carboniferous and Lower Permian localities including, amongst others, the Clear Fork beds of the Texas Permian. In the earlier Texas Wichita beds, however, the only spine type found with pleuracanth remains is that figured by Hussakof (1911, pl. 26, fig. 5) as *Anodontacanthus* (cf. Romer 1942: 227). Here the spine is relatively small. It may show two rows of tiny tubercles distally, but in some cases (as the result of wear) even these appear to be absent. In the present material, pleuracanth spines were found at locality 6, where four specimens were obtained (no. 8528), and localities 1 and 2, where there were fragments of such spines (no. 8527). These are of the "*Anodontacanthus*" type. Specimens lacking the distal portion show typical pleuracanth longitudinal striations but no denticles; one, which is nearly complete, distinctly shows rows of tiny denticles; another, complete to the tip, shows only faint traces of denticles.

Olson (1946: 286-288) discusses the tangled systematic situation in the pleuracanth. He concludes by using the term *Xenacanthus* for the late Carboniferous materials considered in his paper. Since,

however, the only spine material under consideration here is not referable to *Xenacanthus* and is, in fact, closer to *Orthacanthus*, I have preferred to use *Dittodus* as a "blanket" generic name.

Unidentified "Shark" Remains

Unidentified remains of fishes which may have been sharks or bradyodonts of one type or another have been reported from a number of late Pennsylvanian and Dunkard limestones in various instances. Raymond (1910: 148) reports that fish teeth are fairly common in the Ames limestone of the Conemaugh; these may include remains other than the five shark and bradyodont species noted earlier. Condit (1912: 38, 39, 283) reports fish teeth and bones from the Ewing limestone of the Conemaugh near Jewett and Caldwell, Ohio. Tilton (1930: 109, pl. 1, fig. 9) notes "denticles" from the Sewickley limestone of the Monongahela group at Oglebay Park, W. Va., and "sharks' teeth" which appear to be coeliodonts from the Elm Grove limestone of the Washington formation in the same area (Tilton 1930: 11, pl. 3, figs. 2, 74). Stauffer and Schroyer (1920: 146, pl. 12, fig. 36) describe a large spine from shales of the Washington formation at Clarrington, Ohio. Presumably this is a dorsal spine of a shark of some type. It is bluntly triangular in lateral view and bears an ornamentation of small tubercles which are apparently worn.

Cf. *Ectosteorhachis nitidus*

Crossopterygians of the *Megalichthys* type, familiar in the Carboniferous, are known to have survived as late as the Lower Permian in Texas, where numerous remains of *Ectosteorhachis* [*Megalichthys*] *nitidus* have been discovered. Scales comparable to those of *Ectosteorhachis* are present at localities 1 (no. 8522) and 26 (no. 8519). From locality 2 was obtained a clavicle (no. 8521) with the characteristic surface tuberculation of the *Megalichthys* group.

Sagenodus cf. *periprion*

The common lungfish of the late Carboniferous of both Europe and North America and of the early Permian Redbeds of the American Southwest is *Sagenodus*. Remains assignable to this genus are abundant in the present material. Such remains, never found articulated, include dermal bones of the skull roof, parasphenoid and pterygoid, lower jaw, operculum and shoulder girdle, quadrates and tooth plates. Materials are present at localities 1 (head plate, cleithrum, no. 8516), 4 (head plates, parasphenoid, tooth fragment, no. 8518),

6 (abundant remains, nos. 8500-8515, 8543), 26 (head plate, no. 8596), 29 (head plates), 31 (immature tooth) and 37 (plate fragments). *Sagenodus* remains are, thus, present throughout the entire vertical extent of the formations studied, from Conemaugh to Upper Greene. Most notable is locality 6, Cameron, Ohio, in the Washington formation of the Dunkard. Here, a quarry in gray shale and limestone yielded, besides lesser remains of other forms, large quantities of lungfish material.

The dermal plate material is all characteristically *Sagenodus*-like. Watson and Gill (1923:165-188) have described very similar assemblages from the English Coal Measures; Fritsch (1889, pls. 71, 72, 74, 75, 77, 78) has, as Watson and Gill note, described a similar series of plates; and large quantities of undescribed material of this sort are present in the Museum of Comparative Zoölogy collections from the Texas Redbeds. As in these other series, the Cameron materials show numerous variations which appear to be individual in nature or growth stages. Several large and presumably mature opercular bones measure 76, 87 and 83 mm. in greatest diameter and are thus slightly smaller than the opercular in Watson and Gill's restoration (1923, fig. 20). Specimens of mature "parietals" (bone *B* of Westoll's nomenclature, 1949) measure 46, 48 and 51 mm. in greatest length; these are figures well under those of the "parietal," figured by Watson and Gill (1923, fig. 1) in their restoration of the cranial roof of the English Coal Measures *Sagenodus*, and not far from the size of the young adult specimen of their figure 4D.¹ As compared with Texas *Sagenodus* specimens, there appears to be little difference in size of presumably mature elements and no observable morphological differences which might be used for specific differentiation.

There is little dental material except from Cameron, locality 6, in the Washington formation. From here were obtained about sixteen upper and eight lower tooth plates or fragments of plates, two of which are shown in Plate I, figures 1 and 2. Most of the upper plates have approximately ten tooth ridges, with some variation in the development of the small ridges at the posterior end of the plate; two plates, however, have eight ridges. A number of stages in growth and wear are represented, from a small tooth with a length of about 16 mm. to teeth which, while incomplete, appear to have measured

¹ The "× about 3" in the legend of figure 4 of these authors is obviously an error, and should be, as in other figures "× about 2/3."

48± mm. The tips of the ridges in mature teeth are comparable to those described by Romer and Smith for *S. ciscoensis* (1934, fig. 3D). The inner margin of the tooth is gently curved, without the marked angulation figured in *S. ciscoensis* (Romer and Smith 1934, fig. 5E). The lower plates show variations comparable to those of the upper ones. Estimated lengths range from 24 to 48 mm. (no exceptionally young specimens are present in the material). The number of ridges in the few complete Cameron specimens ranges from 10 to 13.

Specific identification is at present impractical, even in the case of the abundant Cameron specimens; *S. periprion* of Texas appears to be closest on present evidence. The writer some years ago (Romer and Smith 1934) attempted an interpretation of the American *Sagenodus* on the basis of the data then available, but abundant new material from the Texas Permian has made it clear that these findings are in need of revision.

Of unusual nature is a specimen, no. 8517, from locality 6. This includes the crushed skull and much of the body of a small vertebrate; the length of the skull as preserved, plus upwards of 20 body segments, is but 6 cm. Of the skull there are numerous fragmentary and disarticulated dermal plates with a shiny enamel-like surface. The body remains show no definite traces of vertebrae but include numerous curved and closely appressed rod-like structures essentially circular in section. At first glance one tends to interpret these as a ventral armor, but they are not jointed nor at all flattened. They thus appear to be the well-ossified ribs of a form in which there was little or no ossification of the vertebrae — a situation true of the lungfishes. The type of preservation is remarkably similar to that seen in the type of the contemporary lungfish *Megapleuron rochei* of Gaudry (1883, fig. 246), although the present specimen is much smaller. I have seen no trace of teeth in the crushed skull; it is probable, although not certain, that we are dealing with a young *Sagenodus* rather than a lungfish of some other type.

Palaeoniscoid Actinopterygians

In late Paleozoic days the commonest inhabitants of fresh waters appear to have been primitive ray-finned fishes, which were the predecessors and, as a group, the remote ancestors of the common teleost fishes inhabiting similar waters today. Such fishes were at one time lumped, for the most part, in the single genus *Palaeoniscus*. With increasing knowledge and the discovery of distinctive generic

types, they came to constitute a family; still later it became clear that they deserved recognition as a major group, the Palaeoniscoidea. Of delicate structure and generally of small size, these fish are usually found in disarticulated form and are exceedingly difficult to identify even generically.

From the region under discussion, I have described (Romer 1942: 218-220, pl. I, fig. 2) as *Amblypterus? stewarti* a large and nearly complete fish from shales immediately above the Upper Washington limestone and thus on the boundary between Washington and Greene formations of the Dunkard. Generic assignment was exceedingly dubious even in this case and is impossible at the present time in the case of isolated scales and small conical teeth, such as comprise all other presumed palaeoniscoid finds from this region. Scales of this sort have been found at localities 1, 2, 3, 16, 26 and 32 in the present material. At locality 26 was found a subrectangular dermal plate (no. 8519) with a delicate vermicular ornamentation, measuring 24 x 20 mm., which suggests an opercular element of a large platysomid. At locality 32 was found a small dentary (no. 8565), 8 mm. long as (incompletely) preserved, and bearing small sharp teeth, about 1/3 mm. long, at average distances of about 1/2 mm. The outer surface is somewhat longitudinally striate but unsculptured. Possibly this represents one of the contemporary palaeoniscoids.

From previous workers we may note that: Price (1927: 225-227, figs. 7, 8, pl. 19; Price, Tucker and Haught 1938: 158) describes small teeth of palaeoniscoid type from the Round Knob formation of the Cone-maugh in the Morgantown, West Virginia region; Condit (1912: 293) reported fish bones and teeth which might pertain to palaeoniscoids from freshwater Conemaugh limestones in Ohio; from the Washington formation, Stauffer and Schroyer (1920: 146, figs. 38, 39) report small teeth which may be palaeoniscoid in the shales associated with the Elm Grove limestone near Beallsville, Ohio; Tilton (1930: 111, pl. 2, figs. 1, 3-6; pl. 3, figs. 1, 3, 5, 6; pl. 4A) describes palaeoniscoid scales and bone fragments from the Elm Grove limestone of Oglebay Park, West Virginia; from the Greene formation of West Virginia, the last writer (1926: 388, 394-395) reports palaeoniscoid scales or teeth from various horizons — the Nineveh shale, Jollytown shale, the shale above the Jollytown coal, the Fish Creek sandstone, Fish Creek shale and the Nineveh limestone; Whipple and Case (1930: 371) note presumably palaeoniscoid scales and teeth from locality L.

Cf. *Saurerpeton obtusum*

Fragmentary remains from locality 1 in the Conemaugh suggest the presence there of a flat-headed, small-limbed amphibian, perhaps antecedent to *Trimerorhachis* of the early Permian and possibly identical with *Saurerpeton* of the slightly earlier Linton channel.

A well-preserved parasphenoid of a small amphibian (no. 8530, pl. 1, fig. 5) is, in general proportions, comparable to that of *Trimerorhachis*, although it is of smaller size; the animal appears to have been, as in that genus, flat-skulled, for the body of the parasphenoid is expanded in a horizontal plane. The bone is embedded in a limestone block; the exposed surface appears to be the ventral one, since the surface of the corpus is nearly smooth and somewhat concave centrally. No carotid foramina are visible. The basiptyergoid articulations were movable and widely separated, facing anteriorly at the tips of processes which extend almost straight laterally from the base of the cultriform process. There is a faint development of a ridge, prominent in *Trimerorhachis*, which passes back laterally on either side behind the basiptyergoid process. The bone is incomplete posteriorly; there is little evidence of "basisphenoid" tubera, but there is present a low median ridge expanding fanwise posteriorly. Much of the cultriform process is preserved. It was expanded anteriorly; more posteriorly it was but moderately expanded and flattened, bearing on its assumed ventral surface a median ridge separating a pair of longitudinal grooves.

The form represented is certainly distinct from *Trimerorhachis*, the characteristic flat-headed form of the later Texas Redbeds, and I know of no other Lower Permian type from that region which is at all comparable. One is tempted to compare it with the Pennsylvanian tetrapods of the underlying Allegheny formation—the trimerorhachoids *Pelion* and *Saurerpeton* and the colosteids *Colosteus* and *Erpetosaurus* (cf. Romer 1947: 86-89, 116-117, 120-121, figs. 15, 16, 22). The bone is most similar to the parasphenoid of *Saurerpeton* in structure and is comparable in size.

From the same locality comes a small amphibian humerus, 14 mm. in length (no. 8562). There is no proof of the association, but it is not improbable that it comes from the same type of animal as the parasphenoid just described. *Saurerpeton* was a tiny-limbed form (cf. Moodie 1916: pl. 17) and the humerus is of an appropriate size for this genus. The entepicondyle is little developed and without a foramen; there is no projecting supinator process.

At locality 1 there are, as noted elsewhere, remains of a small diplocaulid, with a dermal bone structure of a finely pitted type. Not all such sculptured bone, however, pertains to this animal, and one small slab (no. 8559), on which are remains of skull elements otherwise indistinguishable from the diplocaulid, exhibits a small jaw definitely non-diplocaulid in nature. This is seen from the external surface and is incomplete anteriorly. It is relatively long, straight, slender and well-sculptured. Its length, as preserved, is 25 mm. and presumably was on the order of 30 mm. long when complete. It bears over a distance of 12 mm. a row of about 25 slender pointed teeth which show no evidence of labyrinthine folding. This is obviously the jaw of some small labyrinthodont, possibly the same as that to which the parasphenoid described above belongs, although certainly pertaining to a smaller individual.

***Glaukerpeton avinoffi*, gen. et sp. nov.**

The type of this new labyrinthodont is an imperfect skull (no. 8539) from the Conemaugh of locality 1 (fig. 1; pl. 2, fig. 7). This was

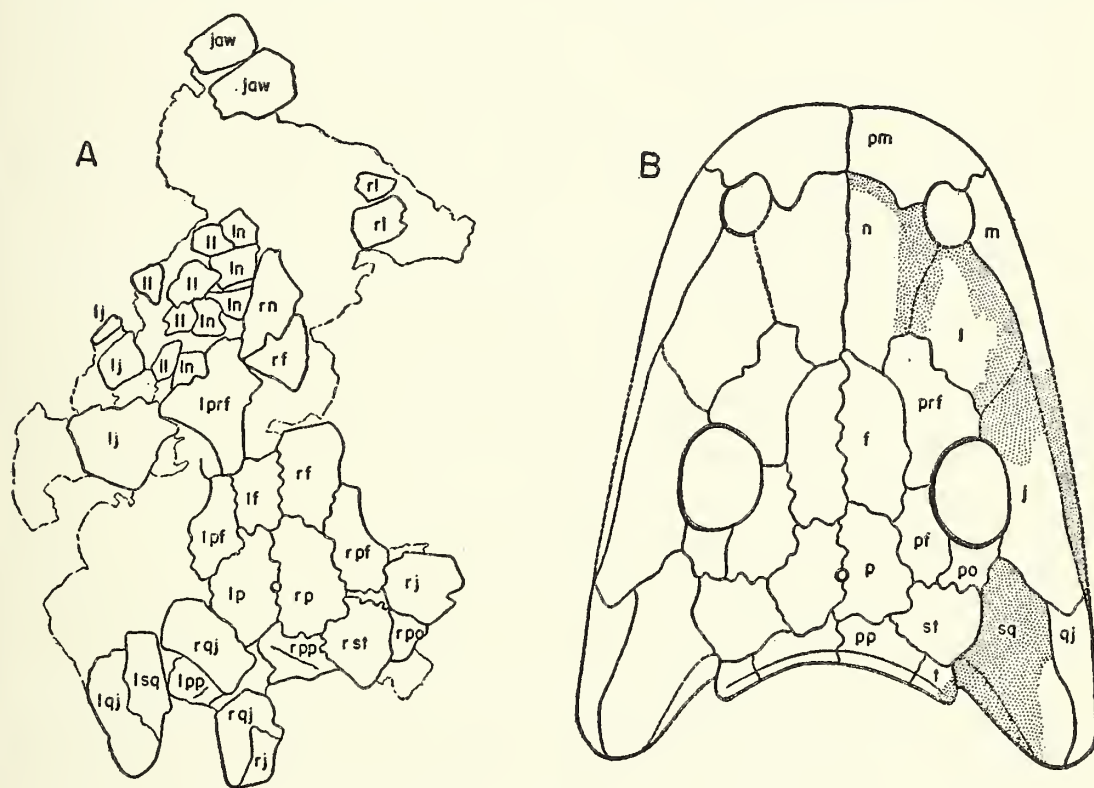


FIG. 1. *Glaukerpeton avinoffi*. A, attempted interpretation of materials of skull roof seen in the type (pl. 2, fig. 7). B, attempted restoration of skull roof pattern; stippled areas on right are portions of roof not present on either side of the specimen. Abbreviations: f, frontal; j, jugal; l, lacrimal; m, maxilla; n, nasal; p, parietal; pf, postfrontal; pm, premaxilla; po, post-orbital; pp, postparietal; prf, prefrontal; qj, quadratojugal; sq, squamosal; st, supratemporal; t, tabular. In A, r and l refer to right and left. $\times 1/5$.

found crushed flat on the surface of a large slab of impure limestone. After cleaning the upper surface, Mr. R. V. Witter performed the difficult task of removing the thin specimen from the block and cleaning the lower surface as well. As can be seen in plate 2, fig. 7, much of the dermal roof is exposed on the upper side; a few additional elements are seen on the under surface, together with crushed remains of palate and braincase.

Much of the skull table is well preserved and essentially in articulated position. The sculpture is more delicate than in the case of *Eryops*, with sharper, narrower ridges separating pits and valleys. The two parietals, with the usual foramen between them, are nearly complete, as are the two postfrontals antero-lateral to them. The large right supratemporal is present in position, and there is no intertemporal — a situation indicating that we are dealing with a rhachitome above the level of organization of the edopsoids and presumably an eryopsid. There are remains of both postparietals, including their occipital flanges, but they are somewhat displaced and partly covered dorsally by other elements. Poor remains of the left tabular are present on the under surface. The postorbital is present on the right side, and its outlines, including the orbital rim, are well seen from below; only a small part of the upper surface is visible. The “cheeks” are, unfortunately, poorly preserved and completely disarticulated. Of the jugal, fragments are present on the right side, lateral to the postfrontal, and a broad section lying below the orbit is present on the left. Both quadratojugals, with fused quadrates, are seen; that of the right side has been pushed over to the left of the skull table and broken in two. A small portion of the left squamosal is found with the left quadratojugal, but there are no other identifiable remains of that important element.

More anteriorly, the posterior portions of both frontals are in position. A piece of bone lying well ahead of the right frontal fits perfectly onto the articulated portion and hence is the anterior part of that bone. When articulated, the median margin lies close to the midline and hence the interfrontal bone characteristic of *Eryops* was not present. The left prefrontal is nearly complete and shifted but little from proper position. Anterior to it are two rows of bone fragments which, with some hesitation, I consider to represent, although incompletely, the left lacrimal and left nasal; to the right of the latter lies a considerable part of the right nasal. Bone fragments near the right anterior corner of the slab appear to be part of the right lacrimal.

On the lower surface of the slab is a stoutly developed premaxilla, comparable in general build with that of *Eryops*, and a long strip of bone (continued by a piece broken off the slab) which appears to represent the greater part of a maxilla. At the far front end of the slab are two lower jaw fragments; the inner surface of the larger fragment faces upward and can be seen to bear (in contrast with *Eryops*) a considerable battery of small coronoid teeth. The under surface of the slab shows various bone fragments representing palate and braincase, but I have been unable to interpret them satisfactorily.

It is impractical to separate the bones of this specimen for restoration; I have, however, made from full-sized photographs, cut-outs of the various pieces preserved and have attempted to reconstruct the skull roof on a clay form. After various essays the pattern restored in figure 1B is that which best fits the material preserved. The position of the suspensorium and the nature of the otic notch are the points of greatest uncertainty, owing to the poor preservation of the cheeks; in other regards, however, it seems probable that the restoration attempted cannot be far from the truth. As restored, the skull has a length of about 26 cm. from snout to occiput.

As noted above, the animal is quite surely an eryopsid, or at least a form closely antecedent to this group (unfortunately the nature of the basal articulation of the braincase and palate cannot be determined). It is not an *Eryops* and is certainly a type otherwise unknown in North America. It is possible that it is generically identical with one of the European eryopsids, although these are later in time of occurrence (cf. Romer 1947: 136-139, fig. 23). However, *Actinodon* can be excluded, because of the fact that the large prefrontal present here would presumably block the lacrimal-frontal contact described in that genus; *Osteophorus* has an interfrontal; these two genera and *Sclerocephalus* and *Onchiodon* as well are short-faced, whereas the fragmentary remains of the "face" in this specimen indicate considerable facial elongation. Distinctions from *Chelydosaurus* of the Bohemian Lower Permian are less clear, but differences in both geological and geographical occurrence render identity improbable. I herewith erect the new genus and species *Glaukerpeton avinoffi*, with this skull as the genoholotype; the specific name in honor of the late Director of Carnegie Museum, Dr. Andrey Avinoff, whose encouragement and support aided greatly in the work of gathering this collection. The genus and species may be jointly defined as a rhachitomous amphibian with the characteristics of the Eryopsidae, face relatively long, lacrimal

not in contact with frontal, no interfrontal, sculpture finer than in *Eryops*.

At the same locality as the type were found several other fragments pertaining to a large rhachitome (no. 8591), presumably *Glaukerpeton*; these include a postparietal and other skull scrap and an *Eryops*-like phalanx 14 mm. long.

Much of the tetrapod material from locality C, at Pitcairn, Pennsylvania, is of amphibian nature; certain elements were reasonably compared by Case (1908) with those of *Eryops*. The material is quite surely that of a rhachitomous type and hence of a form comparable in a general way to *Eryops*. It is, however, quite improbable that this typical Permian genus existed as early as the Conemaugh, the horizon from which this material comes. Further, at least one of the specimens shows distinct differences from *Eryops*. It is, on the other hand, not unlikely that the material pertains to *Glaukerpeton*, a rhachitome of appropriate size and geological occurrence.

The presumed *Glaukerpeton* material from Pitcairn includes: (1) a dorsal vertebra, lacking the spine, showing typical rhachitomous structure (Case 1908: 235, fig. 1, pl. LIX, figs. 5, 6) (no. 1944); (2) a proximal caudal neural spine comparable to that of *Eryops* (Case 1908: 235-236, fig. 2) (no. 1948); (3) a distal neural spine of a rhachitome (Case 1908; pl. LIX, fig. 4) (no. 1947); (4) several ribs (Case 1908: 236, fig. 3, pl. LIX, figs. 7, 8) comparable to the posterior dorsal ribs of *Eryops* (no. 1945); (5) several chevrons (Case 1908: 237, fig. 6, pl. LIX, fig. 2) which Case assigned to the Diadectidae are, however, directly comparable with the chevrons of such a rhachitome as *Eryops* and differ from those of diadectids (and other reptiles) in the large size of the intercentrum from which the chevron arises; (6) other fragments of the axial skeleton which are essentially indeterminate; (7) incomplete acetabular regions of the pubis and ischium of an animal comparable generally to *Eryops*; suggested by Case (1908: 238-239) as fragments pertaining to the pelycosaurs or diadectids; the pubic fragment, however, definitely differing from the pubis of these reptilian types and being typically rhachitomous; (8) a bone which Case (1908: 238, fig. 8, pl. LIX, fig. 1) believed to be the ilium of a reptile. It (8) is, however, identifiable as a sacral rib of the general type found in rhachitomes. In his two figures the head of the bone is at the bottom, the distal (ventral) end of the rib blade at the top; figure 8 is a medial, the plate figure a lateral view of the rib. While the general type of

structure is comparable to that of the *Eryops* sacral rib, there is complete difference in detail, much of which may be seen without lengthy description if the present specimen be compared with the *Eryops* sacral figured by Case (1911: fig. 30).

In sum, all the material noted above appears to be compatible with its pertinence to a single rhachitinous amphibian, but one distinct from *Eryops*; tentative assignment to *Glaukerpeton* is reasonable.

Some fragments of a disarticulated rhachitome skeleton from locality 2 (no. 8538), at practically the same horizon as that of locality 1, may also belong to the same amphibian. These include: (1) a few fragments of cranial bone, comparable in sculpture to the type skull; (2) a labyrinthine tooth; (3) several intercentra comparable in size and general appearance to those of *Eryops*; (4) a characteristic pleurocentrum of rhachitinous type; (5) a badly crushed neural arch (the spine is not preserved); (6) a crushed ulna, comparable in size and proportion to that of *Eryops*; (7) ? distal end of a crushed femur; (8) several flattened structures, apparently parts of expanded thoracic ribs; (9) ventral dermal scales. The material, as far as can be told, is comparable to *Eryops*; but on stratigraphic grounds it is improbable that it belongs to that genus, and it agrees well with the generalized rhachitinous structure expected in the present genus and species.

Eryops* cf. *megacephalus

The common large amphibian of the early Permian Texas Redbeds is *Eryops*. This form is also present in beds of similar age in Oklahoma and New Mexico; it is therefore not unexpected that it proves to be the common large amphibian in the Dunkard as well. Remains indistinguishable from the Texas animal are found in a number of localities in both Washington and Greene formations.

Notable is a specimen, no. 8531, from locality 8 (Ryerson Station) in the Washington formation (pl. 2, fig. 6). This consists of the greater part of a skull seen in dorsal view, embedded in some four blocks of hard limestone. The premaxilla is separated by fissure from the remainder of the skull, as is the left quadrate-jugal region, and the major part of the skull is cleaved down the midline into two blocks. There are many imperfections, and sutures are difficult to find, but first-hand comparison with skulls of *Eryops* from Texas shows great similarity even to details such as the contours of individual elements. With due allowance for fissures between the blocks, the length of the skull from snout to quadrate appears to be about $365 \pm$ mm. The

distance from orbit to naris is 125 mm.; if the ratio of this distance to total length were the same as in Texas specimens, the skull length would be about 385 mm. — a figure comparable to the direct estimate of total length above. The skull is thus rather small — at about the minimum in size — for presumably adult Texas *Eryops* skulls from the typical middle Wichita beds of the Belle Plains and Admiral formations (cf. Sawin 1941: 410), but appears to be of approximately the same size as a number of *Eryops* skulls and partial skulls from lower Wichita deposits (Moran and Putnam formations) in the Harvard collections. Found with this skull was a characteristic *Eryops* neural arch lacking the distal portion of the spine, an atlantal neural arch identical with that of *Eryops*, and a cleithrum with a nearly complete stem, but lacking most of the dorsal blade.

From locality 33 were obtained considerable portions of both upper and lower jaws of a large amphibian, indistinguishable from *Eryops*, together with the parasphenoid and much of the sphenethmoid (no. 8536). Of the upper jaw, anterior portions of both maxillae are preserved, together with the posterior end of the left maxilla. Nearly the whole left lower jaw was present, but the posterior portion is not well preserved; in addition there is present the symphyseal region of the right jaw ramus. Of the left jaw, an anterior portion containing the first 25 teeth (and alveoli) measures 13.5 cm. in length, as compared with a measurement of about 18.4 cm. over the same region for the *Eryops* skull figured by Sawin (1941: pl. 5); this suggests a skull length of 320 mm. The characteristic small symphyseal teeth are present on the jaw. As in *Eryops* of Texas the first three "incisors" in the upper jaw are larger than the teeth following them and there is a development of a "canine" region, tooth 13 being the largest of the maxillary series, with the teeth adjacent nearly as large. A single pleurocentrum is present as well as portions of the dermal shoulder girdle elements.

Locality 28 produced several specimens of *Eryops*. One (no. 8532) consists of the central portion of a skull, exhibiting much of the skull table and interorbital region (pl. 2, fig. 1). The posterolateral margins are broken edges, but on the right side and anteriorly the boundaries are along sutural lines. The "cheek" region — squamosal and jugal — had separated from supratemporal and postorbital, and anterior to the orbit prefrontals, nasals and internasal had separated on either side from the frontals. This separation is highly suggestive of immaturity, as is the situation on the ventral surface. Here, much of the braincase, including the sphenethmoid anteriorly, is preserved but considerably

flattened, as if ossification were not far advanced in the cartilage bone elements. The palate had separated at the basal articulation, a further indication of a juvenile condition. The clear outline of the missing interfrontal is proof that the specimen is one of *Eryops*. If measurements of the parts available are compared with similar measurements of complete skulls, the skull length (to the quadrates) can be estimated as about 405 mm.

At this locality, but in matrix of a different color and hence not necessarily associated with the skull material, was found a cleithrum, clavicle and immature scapulocoracoid (no. 8535, pl. 2, fig. 2). The two dermal elements are nearly complete. They are of small size compared with those of Texas specimens — roughly about three-fourths the linear dimensions of typical Wichita elements. In similar matrix is a very immature scapulocoracoid, crushed flat and ossified only in the scapular region to about the extent of an immature Texas specimen figured by Watson (1919: fig. 1). This cleithrum, clavicle and scapulocoracoid are all of the left side and are not improbably from one individual.

Another animal, however, is represented by the right glenoid region of a scapulocoracoid which, in contrast with the other specimens from this locality, is well ossified and mature (no. 8534). While too incomplete to allow of significant measurements, the specimen is definitely smaller than typical Wichita ones.

Also from locality 28 is a jaw fragment (no. 8582) which may belong to one of the specimens above.

From locality 6 (Cameron) came a specimen (no. 8533) including a nearly complete left maxilla and part of the skull roof and palate adjacent to it. The maxilla contains about 30 teeth and alveoli in a length of 14 cm. This indicates a skull length of about 335 mm. — again a low figure.

At locality 19 was found a fragment of a jaw of a large amphibian, apparently *Eryops*; at locality 21, a tooth of labyrinthine type which may belong to *Eryops*; at locality L, the distal end of an expanded rib, with a terminal cup for attachment of a cartilaginous extension; this agrees with thoracic ribs of *Eryops*.

A number of specific names have been given to specimens of *Eryops* from the Redbeds of the Southwest. Distinctions between them are, however, quite uncertain. It is probable that in the Texas beds "vertical" species differences may be eventually determined, and it is

not improbable that eventually specific differences may be found between Texas forms and those from Oklahoma, New Mexico and the Dunkard area. For the time, however, no valid diagnostic character can be cited and it is preferable at present to assign the Dunkard material to the genotypic species *E. megacephalus*. The Dunkard animal, as noted above, is generally smaller in size than specimens from the Admiral and Belle Plains formations, although this may be in some measure due to immaturity of the material. The size range is, however, not incompatible with that of specimens from the lower Wichita formation of Texas.

"Branchiosaurus" darrahi

I have elsewhere (1939) discussed the history of the branchiosaur concept and pointed out that most supposed branchiosaurs are probably immature or larval labyrinthodonts — most commonly eryopsids. Several specimens of the sort are present in collections from this region. The name "*Branchiosaurus*" *darrahi* was given by me to a larval labyrinthodont, presumably of an *Eryops*-like form, from locality F in the Conemaugh formation (Romer, 1939).¹ It is not improbably the larva of *Glaukerpeton*.

In a soft shale at locality 17 were found remains of a small amphibian skeleton (no. 8561). Because of the fragile matrix and the delicate nature of the skeleton, preservation and preparation of the material proved difficult. Of the head there is most of the table and circumorbital region, seen from below. The skull shape was obviously that of the typical "branchiosaur" — short-faced and large-eyed. The specimen might well be a larval *Eryops*. The orbits are about 4 mm. in diameter, the interorbital distance 2 mm.; the table is broad and measures 10 mm. in width. The skull is incomplete posteriorly; its total skull length was presumably on the order of 15 mm. The reverse of the slab carrying the skull shows a clavicle and interclavicle of the general type seen in *Eryops*; the clavicle measures 9 mm. from the base of the ascending process to its distal termination; as preserved, the interclavicle measures about 10 mm. in length, 9 mm. in width. Imperfect remains of limb bones and ribs are present.

Possibly an immature *Eryops* also is a larger "branchiosaur" specimen from locality 6 (no. 8542). This is represented, in addition to a few

¹I discover to my embarrassment that I had previously (1935: 1635) referred to this specimen as *B. montrosensis*; no description was given and this is hence a *nomen nudum*.

obscure remains, by a partial skull of rhachitomous type, the elements present including postparietals, parietals, frontals, supratemporals, and most of the postorbital series. Unfortunately, the skull becomes imperfect anteriorly not far from the level of the anterior margin of the orbits, so that it is uncertain whether the characteristic interfrontal was present. The oval orbit measures 13 mm. in antero-posterior diameter. The length from the posterior margin of the orbit to the posterior margin of the skull table is 15 mm.; if the face were of "branchiosaur" proportions, the total length would have been about 40 mm.

Undetermined Rhachitomes

Fragmentary remains from a number of Dunkard localities indicate the presence of one or more members of the Rhachitomi of a size considerably smaller than *Eryops*. In Texas, *Trimerorhachis* is the common rhachitome of this order of magnitude. Dunkard remains have been provisionally assigned to this genus by Whipple and Case (1930: 371) and others. But, there is no positive proof of the presence of this Texas form. On the other hand, the material is too fragmentary to warrant, in the absence of clearly distinctive features, the erection of any new genus or genera for its reception.

Much of it consists of vertebral elements. At localities 28 (no. 8568, figs. 2A, B) and M (Tilton 1926: 393) have been found isolated rhachitomous intercentra of the general type seen in *Trimerorhachis*, in which the central portion remained unossified and the element is a slender crescent in end view; a partial intercentrum of the same sort was found at locality 6. At locality 4 was found an articulated series of three vertebrae (no. 8569, pl. 2, figs. 3, 4). These have been so crushed that the ventral surfaces of the intercentra are visible on one side of the small slab containing them; on the other are seen the broken ends of the intercentra, the pleurocentra and the poorly preserved bases of the neural arches. Direct comparison of these vertebral elements with those of *Trimerorhachis* shows differences which render it

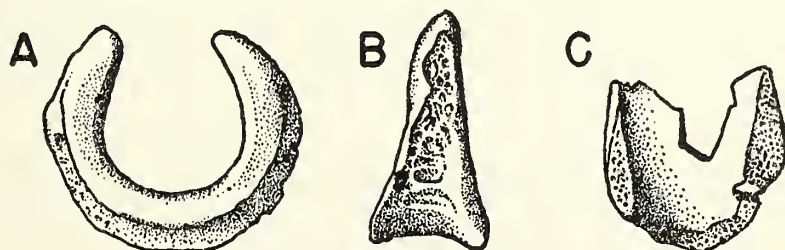


FIG. 2. Small rhachitomous intercentra. A, B, the same specimen in end and side views, no. 8568; C, end view, no. 8575. Natural size.

difficult to identify them generically with that form. There are differences in surface contours and, especially, the Dunkard intercentra are more prominently developed dorsally into a slender pointed termination. These specimens are, however, rather closer to a rhachitome from the lower Wichita formations (Moran, Putnam) of Texas which is as yet undescribed. An intercentrum from locality 6 (no. 8575, in part, fig. 2C) resembles those mentioned above except that a film of ossified bone extends inward to the region of the notochord. Tilton (1926: 391-394, pl. 11, fig. F) described a collection of similar rhachitomous intercentra and an imperfect neural arch from locality J and another intercentrum of this type from locality M (1926: 393, fig. 2); he mentions a caudal vertebra from locality K (1926: 393) which is, however, not described and hence may be of some other nature.

At locality 23 was found a neural arch (no. 8570, fig. 3D) comparable to that of *Eryops* but of much smaller size, although apparently mature. There is no guarantee that this arch belonged to the form or

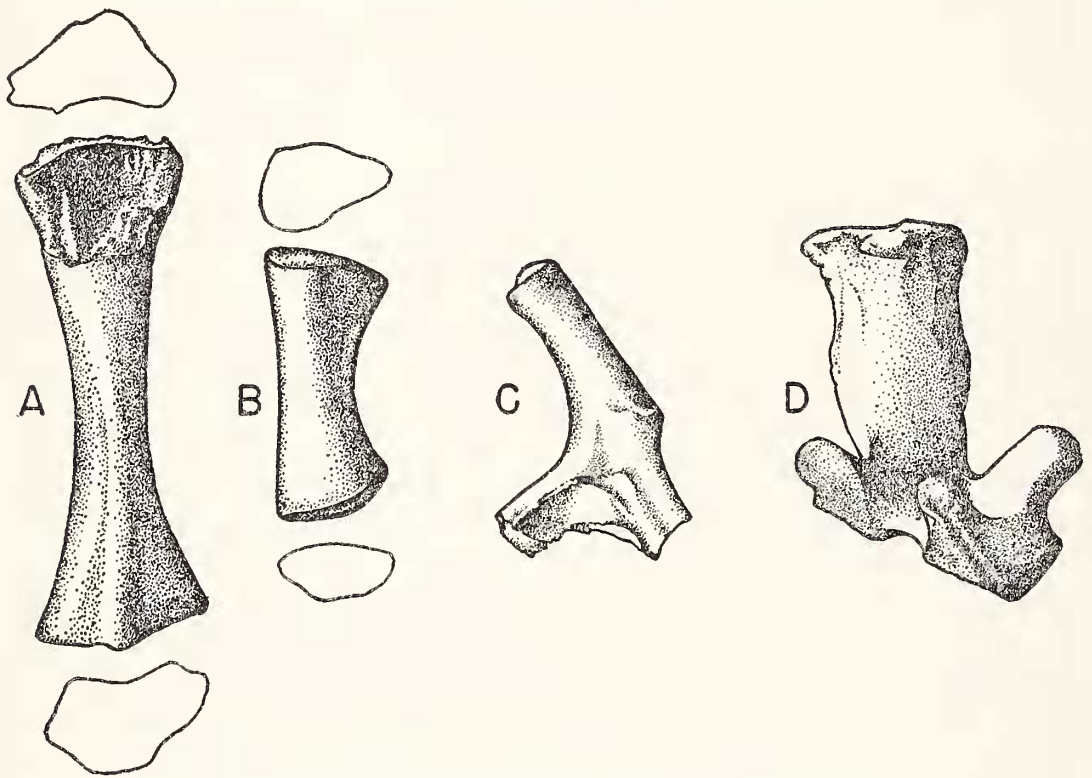


FIG. 3. Remains of small rhachitomes, presumably. *A*, femur, *B* (?) tibia, *C*, ilium, all from locality L (material at Marietta College); *D*, neural arch, no. 8570. *A-C*, $\times 4/3$; *D*, $\times 1$.

forms to which the intercentra just described pertain; it will be noted that the neural arch of *Trimerorhachis* is of a very different character.

From locality 5 was recovered the greater part of a jaw of rhachitomous type (no. 8571), 112 mm. long as incompletely preserved, and

probably 140 mm. long when complete. There is a coarse sculpture, but little detail can be made out. The specimen is of dimensions appropriate to the vertebral material described above. In size, it is comparable to *Trimerorhachis* but there is, in contrast with that genus, a well-developed "coronoid" region which rises well above the general jaw level. A poorly preserved jaw which may be of similar type is present, together with a clavicle and other sculptured bone, at locality 15 (no. 8572), and at locality 37 a small fragment of upper jaw (no. 8613) of appropriate size. Specimen no. 8592 consists of obverse and reverse of the angular and articular regions of a jaw of *Trimerorhachis* size, with a coarse external sculpture. It is probably from locality 1, and hence much earlier in time than the Dunkard specimens described in this section, but the locality record is uncertain.

The material at Marietta College from locality L, tentatively identified as *Trimerorhachis* includes, as well as sculptured plates of uncertain nature, several small limb and girdle bones shown in figure 3 A-C. These may belong to a small rhachitome, but this is not certain.

***Diploceraspis burkei* gen. et sp. nov.**

"Horned" nectridian amphibians are common in the Upper Carboniferous of both Europe and North America, and *Diplocaulus*, a large and long-horned form, appears in the late Pennsylvanian of Illinois and is a common member of the Clear Fork fauna of the Texas Permian. Members of this group of amphibians are common also in the Pittsburgh region; their remains are the most frequently encountered of any animal type and are present in about half of all collecting localities. The history of the group appears, however, to have differed somewhat in this eastern region, with the parallel development of a long-horned type comparable with but distinct from *Diplocaulus*.

Materials of this animal are most common in the Greene formation of the Dunkard. A considerable number of fragments of vertebrae and sculptured bone were found at locality 26; no other tetrapod remains were found at this locality, and hence it is not unreasonable to assume that the *Diplocaulus*-like materials from this site belong to a single form. Locality 26 lies in a limestone presumed to be the middle Rockport limestone of the Greene formation. Stratigraphically close, in the Rockport limestone series, are localities 18, 20, 21, 23, 24, 27, 28, 29, 30, and L, also containing materials of similar character. The description following will be mainly based on the material from

locality 26, but that from the other localities listed will be used to fill in details.

There is no complete skull; the greater part of a skull, seen in dorsal view, is present in no. 8551, but with the "horn" tips missing and the anterior part of the skull destroyed (pl. 2, fig. 5). Specimens 8552 (pl. 1, fig. 8), 8548 and 8553 (the last from locality 28) include nearly complete "horns"; various other skull fragments are present in the material. Almost all specimens are seen in dorsal view (except for distal portions of the "horns"). Using all available data, the skull

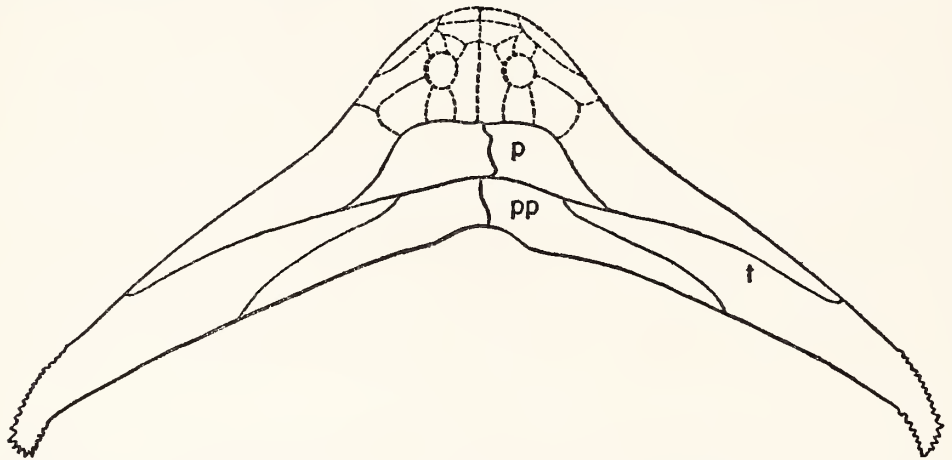


FIG. 4. Attempted restoration of skull of *Diploceraspis burkei*. The central and anterior portions of the skull are entirely hypothetical. One half the size of typical specimens. Abbreviations: *p*, parietal, *pp*, postparietal, *t*, tabular.

may be restored with fair safety on the pattern seen in figure 4. In no specimen is the anterior part of the skull preserved. The animal is obviously of the diplocaulid pattern in skull proportions, with quite long and slender tabular "horns." These are directed more laterally than in typical *Diplocaulus* material; the anterior margins of the two "horns" when prolonged meet at an obtuse angle of about 110°, whereas the typical Texas *Diplocaulus* gives a figure generally well on the acute side of 90°. The back margin of the head shield shows a concave curved rim above the region of the occipital condyles much as in *Diceratosaurus* and *Batrachiderpeton* and in contrast with *Diplocaulus*, which has a smoothly rounded posterior margin. The slender tips of the "horns" are curved and, as shown by no. 8552, bear a series of sharp serrations on the convex margin. There is no positive proof as to the direction of curvature of these tips, but it is reasonable to assume that they curved posteromedially rather than laterally.

The sculpture is in the form of a series of tiny pits which show little of the usual amphibian tendency toward oval elongation, even

when distant from a presumed center of ossification. The average diameter of the pits is on the order of one-half millimeter. This is sculpturing of a much finer sort than in the case of the Texas *Diplocaulus*. It is in part attributable to absolute size differences in the individuals concerned. However, an immature Clear Fork *Diplocaulus* which is of approximately the same size as the present specimens has pitting with an average diameter nearly twice as great as in this material.

Little can be made out as to sutural pattern except that there appear to be, as in *Diplocaulus*, very broad postparietals, extensive tabulars, and broad parietals and supratemporals. No data are present as to palatal structure or braincase, but a well-preserved atlas vertebra (fig. 5C, D) proves the existence of distinct paired occipital condyles, as in *Diplocaulus*.

Specimen no. 8551, when restored, measures about 75 mm. from the mid-point of the posterior margin to "horn" tip. Specimen no. 8552 was apparently slightly larger, on the order of 85 mm. for this measurement, and specimens no. 8548 and no. 8553 were probably of this or a somewhat larger size. Since there is thus a general agreement between specimens, it may be reasonably assumed that we are dealing with "adult" animals. These individuals are far below the typical Texas Clear Fork *Diplocaulus* in size, although in these Redbeds occasional small and presumably young individuals are encountered.

Partial jaws are present in nos. 8552 and 8553. In the former the jaw is visible from the inner surface, with the anterior end incomplete; in no. 8553 an adhering film of limestone makes detailed preparation difficult. The ramus of no. 8553 is 30 mm. in greatest length, that of specimen no. 8552, 26 mm. as (incompletely) preserved. The proportions of the jaw are much as in *Diplocaulus*. The ramus is flattened ventro-laterally and sculptured; it is strongly inturned anteriorly toward the symphysis. Posteriorly the jaw is less flattened and attains a modest height, with a distinct "coronoid process." There is a retroarticular process. On the inner surface there is no indication of a mento-meckelian fenestra, but a broad groove extends antero-posteriorly along this aspect; within this groove the bone shows a spongy surface through which there appear to extend a number of small openings. Sutures were not discovered. The dentition is not completely preserved in either specimen; it appears probable that there were 12-15 fairly large subequal marginal teeth (+alveoli), in contrast with a larger number of tiny teeth in *Diplocaulus*. Individual

teeth where well preserved have a length of about 1.5 mm., and a basal diameter of somewhat less than a millimeter. On one specimen stumps are present of two teeth of good size internal to the marginal tooth row and close to the symphysis. On the other there is some indication of coronoid teeth, but the evidence is not clear.

There are a few postcranial remains. At locality 20 a limestone block exhibited a naturally weathered clavicle, nearly complete (no. 8555). The flattened ventral surface bears a punctate ornament finer than that of the skull roof, with indications of radiation from a center near the base of the ascending process. This surface is sub-triangular, comparable in shape to that of *Diplocaulus*; it measures 19 mm. in anterior-posterior length, 14 mm. in breadth. There is a slender ascending process which as preserved is 8 mm. in length. There are in the collections several other incompletely preserved plates which may be remains of clavicles or interclavicles. There are no further identified remains of girdle or limb elements.

Vertebrae (none, however, articulated) are present at almost all of the Greene localities listed above (fig. 5). Of dorsal vertebrae, eight

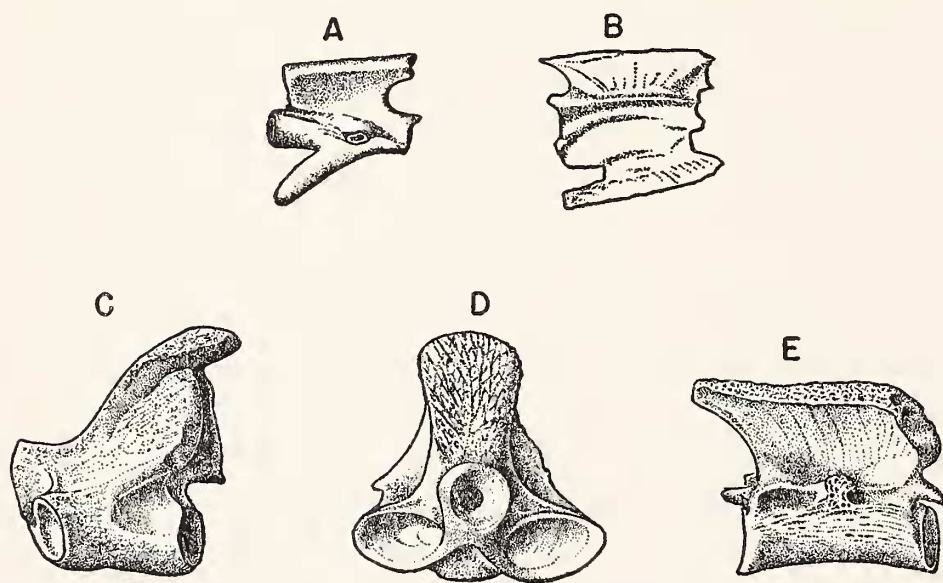


FIG. 5. *Diploceraspis burkei*, vertebrae. A, presumed anterior caudal, no. 8555; B, typical caudal, no. 8550; C, D, "atlas" in left lateral and anterior views, no. 8553; E, typical dorsal, left lateral view, no. 8549. A, B, E, $\times 4/3$; C, D, $\times 2$.

have measurable lengths of 5, 7, 7, 7, 11, 11, 13 and 14 mm. There are, further, four fairly complete caudals, with lengths of 8, 8, 9 and 10 mm. There is thus considerable disparity in length, part of which, at least can be attributed to growth stages and regional differences.¹

¹ Note the great disparity in length along the presacral series of *Diplocaulus* as seen, for example, in fig. 3 of Douthitt (1917).

These measurements are, like those of the skull, far below those of presumably adult Clear Fork *Diplocaulus* specimens. The presacrals show, in general, a typical pattern for this group. The surface of the centrum shows, where well preserved, a somewhat rugose, vermiculate pattern comparable to that of *Diplocaulus*. There is, however, a notable difference. In *Diplocaulus*, the dorsal neural spine develops as an unornamented ridge bearing a characteristic pit. In the present form, the dorsal neural arch is preserved and visible in five instances; in each the arch is strongly sculptured, as it is in *Diceratosaurus* — a sculpturing much more pronounced than the general rugosity of other parts of the vertebra.

Three of the four caudals from the Carnegie Museum localities show a structure quite comparable with those of the proximal half of the *Diplocaulus* tail, and a short series of caudals from locality L, although poorly preserved, is similar. A fourth vertebra in the Carnegie Museum collection from locality 20 (no. 8555) is of unusual character (fig. 5A). It bears a neural arch of "caudal" type and a haemal arch. The haemal, however, instead of being that characteristic of the tail generally, is a rod directed postero-ventrally. It is suggested that this element is a caudal from an immediately postsacral position.¹

It is obvious that in this Dunkard amphibian we have a form related to *Diplocaulus* of the contemporary Texas Redbeds, but notably distinct from it in its neural arch sculpture. This is herewith designated *Diploceraspis burkei*, gen. et sp. nov. with no. 8551 as the genoholotype.² Apart from the feature of neural arch sculpture, distinctive characters which may be either generic or specific include the long and slender "horns" which are directed more laterally than in *Diplocaulus*; the recurved and spiked nature of the horn tips; the delicate sculpture of the dermal roof; the teeth, relatively larger and less numerous than in *Diplocaulus*; and the relatively small size of the animal, typical representatives being somewhat less than one half the size of the "normal" Clear Fork *Diplocaulus*.

As both Jaekel (1903) and Watson (1913) have pointed out, *Diplocaulus* was preceded by and descended from Carboniferous forms with shorter "horns." It is probable that *Diplocaulus* and *Diploceraspis*

¹ Although this does not agree with Case's description of a vertebra of *Diplocaulus* from a presumably similar position (Case 1911: 89).

² The specific name in honor of Mr. John J. Burke, leader of the expeditions on which this material was collected.

have evolved in parallel fashion from distinct Carboniferous ancestors. The presence of sculptured neural arches suggests that the latter genus has descended from *Diceratosaurus*, common in the Upper Pennsylvanian of this very region. *Diplocaulus* (already present in the late Pennsylvanian of Illinois) might have developed from one of the other typical Carboniferous genera — *Cephalerpeton*, for example.

The description of *D. burkei* above was based on material from localities in the Rockport limestone horizons of the Greene group. Remains which may pertain to this form are present at both higher and lower Dunkard levels. In the upper Greene, skull fragments and a dorsal vertebral centrum, 12 mm. in length, were found at locality 35 and a dorsal centrum 8 mm. long at locality 37. Most puzzling are two specimens from locality 36 (no. 8547). Preserved as hollow molds in slabs of limey sandstone are fragments of spines or hornlike structures, one of which is shown in plate 1, figure 6. The structure was much flattened, with a thickness as preserved of about 3 mm. as contrasted with a width of about 1 cm. Both sides bear an ornament closely comparable to that of a *Diploceraspis* horn and one tends to assign these specimens to *D. burkei*. But, as can be seen from the figure, there is very little tapering from one end of the segment preserved to the other. If this is a "horn," it was seemingly one of inordinate length. I have tried to imagine these "spines" as belonging to some other type of animal (or plant) but with little success.

Lower levels in the Dunkard have yielded fragmentary remains of *Diploceraspis*: a sculptured bone fragment, possibly a clavicle, from locality 16; from locality 14, an incomplete stemmed clavicle and a dorsal vertebra 10 mm. long; from locality 13, dorsal vertebrae 10 mm. and 9 mm. in length and a skull fragment; sculptured bone fragments including part of a "horn" from locality 7; and a dorsal vertebra with a length of about 10 mm. at locality 6. This last specimen is perplexing, for it lacks—in contrast with all other dorsals of this species—sculpturing on the neural arch. Are there, perhaps, two diplocaulid types in the Dunkard? The situation is less puzzling when it is noted that there is but a single rib facet present and that, hence, the specimen is from the posterior dorsal region. Caudals, in contrast to typical dorsals, are non-sculptured; a shift occurred at some point anterior to the tail; one or more posterior dorsals might lie distal to the point at which arch sculpture disappeared. There is at present no reason to believe that any of the Washington or lower Greene diplocaulid materials belongs to a form other than *Diploceraspis*.

***Diploceraspis conemaughensis* sp. nov.**

The nectridian material from locality 1 is disappointingly fragmentary. In it are a number of diplocauloid dorsal vertebrae with measurable lengths of 8, 7, 7, 5, 4 and 4 mm. If these are representative, we are dealing with an animal of smaller size than the Dunkard form. The neural arch is seen in four cases; in three it is sculptured (the fourth is presumably a posterior dorsal) and hence suggests *Diploceraspis* of higher horizons or, alternatively, *Diceratosaurus* of the underlying Allegheny group. There are present in the Soho material some eight small slabs (nos. 8544-46) bearing fragments of sculptured amphibian bone with a punctate pattern similar to that of the Dunkard *Diploceraspis* but rather finer and also similar to that of *Diceratosaurus*. I am quite unable to determine the skull pattern from the disarticulated plates present, and the mere presence of a finely punctate sculpture does not guarantee that we are dealing with a *Diploceraspis*. Two specimens are, however, significant. No. 8546 consists of a flattened piece of bone, nearly free of matrix, which is sculptured on both surfaces and represents part of a tabular "horn." It is incomplete at the tip but even so indicates a "horn" development much greater than that of *Diceratosaurus* and nearly as marked as in *Diploceraspis burkei*. The margins of the "horn" are imperfect, but indicate a decrease in width from about 17 mm. to 6 mm. in the length of 3 cm. preserved. This is a slightly stubbier "horn" type than in the Dunkard form, but far closer to it than to *Diceratosaurus*. A fragment belonging to no. 8545 consists of a "horn" tip; this is recurved, but less so than in *D. burkei*, and lacks the prominent spines seen in that form.

Although the material is unfortunately far from adequate and the probable differences from the Dunkard form small, it seems advisable to recognize the Conemaugh diplocaulid as distinct. It is herewith designated as *Diploceraspis conemaughensis* sp. nov., with the "horn" fragment no. 8546 as the holotype, distinguishable at present from *D. burkei* by smaller size, somewhat lesser "horn" attenuation, and a lesser degree of curvature and spinescence at the "horn" tip.

If *Diploceraspis* evolved from *Diceratosaurus* of the Allegheny group, the "horn" attenuation indicated by the Conemaugh material shows a rapid, early evolution of the genus, followed by relative stagnation. The development of *Diploceraspis* paralleled that of *Diplocaulus*. But, while we do not know the skull form of the *Diplocaulus* from the

Pennsylvanian of Illinois, the few known Wichita specimens of *Diplocaulus* are quite "short-horned." The evolution of elongate "horns" may have proceeded more slowly in the *Diplocaulus* line.

***Lysorophus dunkardensis* sp. nov.**

The small worm-like amphibian *Lysorophus* (originally described from the late Pennsylvanian of Illinois) is a common animal in the Clear Fork Permian of Texas (although locally absent in the earlier Wichita beds of that region). It is now recognized that *Cocytinus* and *Molgophis* (including *Pleuroptyx*) of the Allegheny formation of the present region are earlier representatives of this group (Watson 1929: 249; Romer 1930: 81; Steen 1931: 885). It is thus natural to expect that lysorophids would have persisted into the latest Carboniferous and early Permian of the Pittsburgh region. This proves to be true; lysorophids are moderately abundant in the material under study. They are notable, however, for a great range in size and, despite confusion which may be caused by the finding of immature specimens, it appears probable that several distinct forms occur here.

The most "normal" lysorophid is one which appears to be present in a series of half a dozen Dunkard localities and may represent an animal comparable to that of the Texas Permian. It is considerably larger than the characteristic *Lysorophus* of that region, although Olson (1939) has noted the presence there of "outsized" specimens. A well-preserved and maturely ossified centrum from locality 37 (no. 8581) shows a typical lysorophid structure; it measures, however, 9 mm. in length and 8 mm. in end diameter as contrasted with much lower figures generally for the Texas *Lysorophus*. I herewith designate this form as *Lysorophus dunkardensis* sp. nov. with the vertebra mentioned as the holotype; for the time being, its greater size is the only specific character available.

Several other Dunkard specimens may be specifically identical. No. 8584, from locality 34, and no. 8585, from locality 35, consist of vertebral fragments of similar size.

Whipple and Case (1930: 371) report vertebrae similar to those of *Lysorophus* from locality L. This is reasonable, but I did not find such vertebrae in the material available to me. No. 8586 from locality 1 consists of a slab of limestone exhibiting a series of stout curved ribs and an imperfect vertebra resembling those of the species in question.

No. 8587 from locality 3 shows a cluster of similar ribs and sections through vertebrae apparently of a lysorophid nature. If these specimens are correctly assigned, *Lysorophus dunkardensis* is present throughout the series under consideration, from Conemaugh to Greene.

A puzzling specimen from locality 6 (no. 8590) may be mentioned here. This consists of obverse and reverse slabs of shaly clay showing a tangled mass of countless tiny curved ribs and, less clearly, other skeletal remains; all appear to belong to a single animal. These are poorly preserved remains and impressions of vertebrae of lysorophid type, about 4 mm. in length. This specimen is thus intermediate in size between *L. dunkardensis* and a tiny form next described. Are all three growth stages of a single type? As noted below, the small *L. minutus* appears mature, however. In contrast, in the present specimen the vertebral remains are very poorly preserved, despite the well ossified condition of the ribs. Tentatively the specimen may be considered as an immature individual of *L. dunkardensis*.

***Lysorophus minutus* sp. nov.**

In a slab of limestone from locality 30 were found obverse and reverse impressions of much of the skeleton of a tiny elongate snake-like amphibian (no. 8564, pl. 1, fig. 7). A portion of the skull is present and two series of vertebrae: a major series thrown into an S-shaped curve and a second, shorter, series partially overlapped by this. The specimen is crushed and not too well preserved, so that neither in skull nor in backbone have I been able to make out details of structure with any assurance. Of some three types of much elongate lepospondylous amphibians characteristic of the late Paleozoic, the *Ophiderpeton* and *Dolichosoma* groups are eliminated by the fact that the specimen shows quite stout, if short, curved ribs (the articular region is not seen); there is no certain trace of ventral armor. It thus appears likely that the specimen is a member of the *Lysorophus* group, and the general impression one gains of vertebral structure is in agreement with this conclusion. It is, however, of small size compared with the typical Texas form; the centra average somewhat under 2 mm. in length, which is rather less than half the size of the Texas representative of the genus or of the type material from the late Pennsylvanian of Illinois, and still smaller in comparison with *L. dunkardensis*. The size, however, is about that of *Cocytinus gyronoides* of the Allegheny formation of the present region — a predecessor and presumed ancestor

of *Lysorophus*. Since the specimen is well ossified, it is difficult to consider it as an immature *L. dunkardensis*. It is herewith designated as *L. minutus*, sp. nov., with its small size as the only specific criterion known at present.

***Megamolgophis agostinii* gen. et sp. nov.**

This giant lysorophid is the most striking of Permian novelties in the present material. In the Allegheny Group of the Pennsylvanian in this same region, there were present not only the small lysorophid *Cocytinus* but also a considerably larger form, *Molgophis*.¹ The *Molgophis* line continued into the Permian of the region to end with the form here described as *Megamolgophis* — an animal quite unknown in other Permian deposits.

The two most important specimens are nos. 8583 and 8614, the former from locality 28 consisting, in the main, of 27 isolated but well preserved vertebrae, the latter, from locality 11, including the partially articulated remains of what appears to be a single individual (fig. 6), with about 70 vertebrae present. Although most of the materials of these two finds belong to *Megamolgophis*, there is some admixture of other forms; scraps of *Eryops* are found in both, and pieces of sculptured *Diplocaulus* bone in no. 8583. Less important specimens which appear to belong to this snake-like amphibian include a rib-head from locality 35 (no. 8588), a natural mold of a vertebra from locality 36 (no. 8589), poorly preserved vertebrae from locality L which were tentatively referred to *Theropleura* by Whipple and Case (1930) and, doubtfully, a weathered vertebra from locality 1 (no. 8610).

This was an animal of considerable size. The mean length of sample vertebrae from the two major specimens, measured along the ventral surface, is approximately 15 mm. We do not know the number of vertebrae, but Steen cites a specimen of the related *Cocytinus*, apparently complete, with 81 vertebrae. If the count were here the same, the length (adding an allowance for the head) would be about 130 cm., or well over four feet. This is a figure quite in contrast with the length of but a few inches of *Cocytinus* or *Lysorophus*. The length

¹ This genus and a second, *Pleuroptyx*, were described by Cope on the basis of vertebrae. The writer (1930: 106-108) noted that the two appeared to be identical and suggested that these vertebrae pertained to the labyrinthodont *Colosteus*. Steen (1931: 882-885) correctly pointed out that this was not the case, and that the *Pleuroptyx* vertebrae were of lysorophid type. She did not, however, mention *Molgophis* (except for the small "species" *M. wheatleyi* which is a *Cocytinus*).



FIG. 6. *Megamolgophis agostinii*. Part of a specimen presumably of one individual, showing numerous characteristic vertebrae, ribs, partial jaw, etc. No. 8614. $\times 1/3$.

is about that of the common American blacksnake; however, the girth (as noted later) was considerably greater and comparison with a Florida diamondback rattlesnake might perhaps be more apt. Vertebrae of two Allegheny specimens of *Molgophis* approximate the present form in size, but these are exceptional; six specimens give a mean vertebral length of approximately 10 mm. for that genus.

In the vertebrae (fig. 7), the centrum is suturally separate from the neural arch in all cases seen; the union between them was a loose one, and they disarticulate readily. There is no trace of intercentra and the fit between adjacent centra is such that these elements were surely absent. The centra have an appearance superficially like those of many primitive reptiles. They are essentially spool-shaped structures, deeply amphicoelous and notochordal, with an end diameter which is on the average about 85 per cent of the length. In almost every well-preserved centrum the posterior rim bears, high up on the lateral margin, a distinct projecting flange, facing posteriorly, to receive the capitulum of the rib of the following vertebra. Dorsally, there is a longitudinal groove, deepest at mid-length, which lies in the floor of the neural canal. On either side is a broad oblong surface for articulation with the neural arch. This generally occupies the anterior two-thirds of the length of the centrum, facing upward and slightly outward; it is usually nearly flat, but turns slightly upward posteriorly.

The basic pattern of the centrum in *Lysorophus*, *Cocytinus* and *Molgophis*, as described by Sollas (1920), Schwarz (1908) and others, is that of an hourglass or spool surrounding the notochord, from which project (in addition to the arch bases) a pair of lateral longitudinal ridges and a ventral ridge which exhibits to some degree a duplex nature. In *Megamolgophis* we see a strong tendency for elaboration of this pattern of longitudinal ridges, particularly in the ventral ridge system. In a fair proportion of the vertebrae preserved, the construction is relatively simple, consisting of a pair of apposed but distinct ventral ridges and a pair of lateral ridges, with a deep pocket on either side between ventral and lateral elements (fig. 7D). In most vertebrae the lateral pocket is retained but the ventral ridge system is more complex. A median ridge, single or double, may appear between the elements of the ventral pair, or each ventral ridge may be present in double form (fig. 7E). In a stage of greater complexity, the lower aspect of the centrum, between the lateral pockets, becomes a continuous surface in which 8 or 10 ridges may be imperfectly distinguished (fig. 7F).

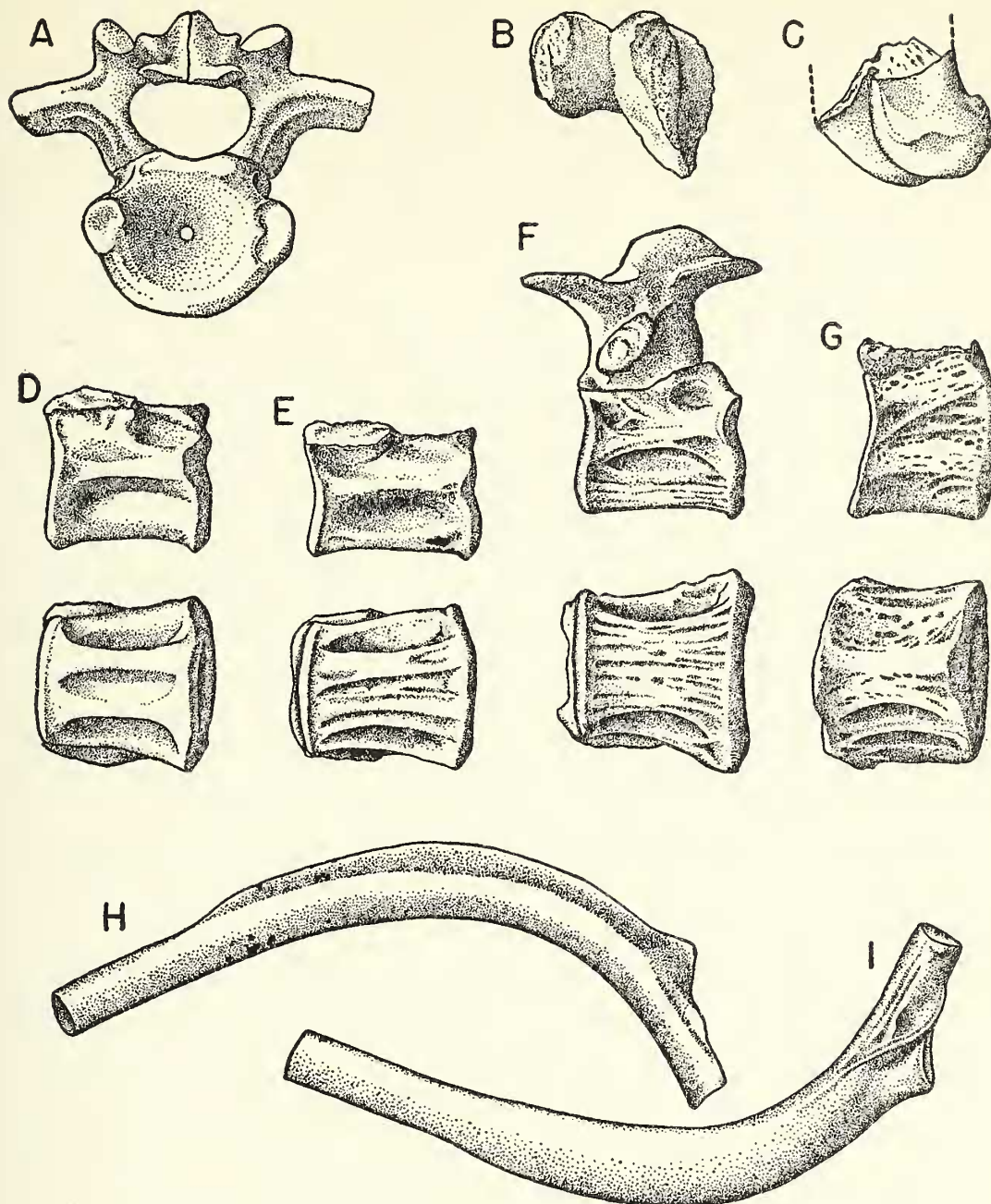


FIG. 7. *Megamolgophis agostinii*. A, posterior view of a vertebra; composite, arches and centrum not definitely associated. B, C, ventral and lateral views of an incomplete quadrate. D-G, left lateral and ventral views of vertebral centra, to show degrees of complexity of development of ridge system of centrum. F is lateral view of the same vertebra shown in A. H-I, internal and external views of a rib of the left side (composite of two specimens). B, C, no. 8614; others no. 8583. Natural size.

A final stage (represented by 4 vertebrae of 27 in specimen no. 8583) is one in which even the lateral pockets and the lateral ridges lose their individuality and the entire outer surface of the "spool," from one arch attachment to the other, shows a considerable series of low longitudinal ridges between which there seldom develop grooves of any depth (fig. 7G). These last vertebrae are relatively short and stout,

with a mean length of 12.7 mm. and a mean diameter of 15.2 mm.; this in strong contrast with general lengths on the order of 15 mm. and diameters of about 13 mm. In these short vertebrae the surfaces for arch attachment extend nearly the length of the centrum; there is a variable development of a forward projecting ventral "lip;" in two of the four centra of this type in no. 8583 there is no development of a facet for the capitulum.

There is nothing to indicate the position in the articulated column of the types of centra described. The last type mentioned is not improbably that of the anterior cervical region, and it may be that there was a progressive simplification of the ridge system along the "trunk" and tail; but, on the other hand, the short vertebrae might possibly be those of the sacral and proximal caudal region.

In a long-tailed animal we would expect a gradual tapering of the centra in diameter and, to a lesser degree, in length, in the distal caudal region. But, among the numerous vertebrae in no. 8614 there is none which appears to be markedly smaller than the average, and in no. 8583 only one notably small centrum; this (somewhat imperfect) has a length of about 13 mm. but a diameter of only about 11 mm. It may be that in both specimens the distal portion of the tail was lost, but quite possibly the tail remained stout to a point near its termination.

Neural arches, many articulated, are numerous in no. 8614, but are poorly preserved. In no. 8583, upward of a dozen arches are well preserved, but are disarticulated. They show an essentially uniform pattern (fig. 7A, F). As in *Lysorophus* the members of each pair of arches are separated; presumably they were connected in life by an intervening plate of cartilage. The stout arch pedicel rises upward with little change in thickness to the level of the zygapophyses. Here, the inner surface curves medially to form the roof of the neural canal. Each arch carries anteriorly on its outer surface a well-developed transverse process, extending outward and somewhat forward from the general level of the arch to a distance of 5-8 mm. and terminating in an oval surface for articulation with the rib tubercle. A system of low ridges may extend on to the arch from the base of the transverse process, and in two of the arches preserved, a stout ridge, bearing a presumed continuation of the articular face, runs anteroventrally in the direction of the capitular articulation on the adjacent vertebra.

The anterior zygapophyses are elongate anteroposteriorly and concave in transverse section, extending forward from a point above the base of

the transverse processes. The posterior zygapophyses are correspondingly elongate and convex in section and extend far posteriorly. Above the posterior zygapophysis each neural arch rises, thinning above, into a low "spine" with a curved upper margin. The entire inner surface of this area is flattened for apposition to the arch of the opposite side. The arches as a whole are closely comparable to those of *Lysorophus*.

A large number of ribs are present in no. 8614, but they are poorly preserved; in no. 8583 none of the ribs is complete, but there are numerous well-preserved fragments (fig. 7H, I). The rib-heads show distinct, subcircular capitula and tubercula; the capitulum does not show the subdivision figured by Sollas (1920, fig. 41, i) in *Lysorophus* or Schwarz (1908, fig. 11) in *Molgophis*. A main rib axis, subcircular in section, extends from the capitulum along the lower margin of the strongly curved proximal portion of the rib. As in many early tetrapods a thin flange extends backward externally from the main shaft of the rib, giving the rib, in section, a figure like that of a musical half note (cf. Sollas 1920, fig. 44, section 86). This flange commences proximally at the tubercle and extends in some instances, at least, about three-fourths the distance from the tubercle to the rib termination, gradually merging into the rib shaft distally. In most of the rib fragments available, the flange is narrow, extending but three or four millimeters beyond a rib axis of about the same diameter. In one rib fragment, however, the flange is about twice as broad, the total breadth of the rib reaching 11 mm.; this gives a configuration resembling that in *Pleuroptyx*. Presumably the variations are regional; possibly, as in more normally built tetrapods, the broader ribs lay in the region adjacent to the shoulder.

A second flange seen in the proximal portion of various specimens of the *Megamolgophis* rib, is, as far as I am aware, a unique feature. This extends anteriorly from the shaft. It is much shorter than the posterior flange; it rises abruptly at a point just proximal to the tubercle, reaches a maximum development of about four millimeters opposite the tubercle, and sinks into the general level of the shaft three centimeters or so distal to that point.

The distal part of the rib shaft is subcircular in section and nearly straight; in several instances where the distal end is preserved, it is seen to be cupped, presumably for the attachment of a cartilaginous ventral rib segment. In the absence of complete and articulated material, no accuracy can be attained in the matter of rib articulation; it appears probable, however, that the width of the body between the

farthest lateral extension of the ribs was not far from ten centimeters. The height from the ventral ends of an ossified rib to the top of the neural arch was approximately six centimeters. Three centimeters or so should be allowed for the curvature of the belly; a subcircular body section is indicated.

There are no articulated limb materials, but several bones appear to be limb elements: for example, a bone in no. 8614 has the appearance of a femur, with a length of 38 mm.; a short stout bone, 30 mm. in length is suggestive of a tibia in no. 8583. It seems certain that, as in *Lysorophus*, the limbs were extremely small.

Specimen no. 8614 includes the articular portion of a quadrate (fig. 7B, C), showing two highly developed articular keels, each curved to about 180° and separated by a deep groove. Further skull material is interesting but confusing. This consists of a mass of crushed and broken material forming part of no. 8614. It exhibits on one surface sculptured dermal bones, obviously part of a skull roof (fig. 8A), and on the other aspect various bony materials presumably cranial in nature, including an incomplete maxilla and fragments which appear to be part of a dentary.

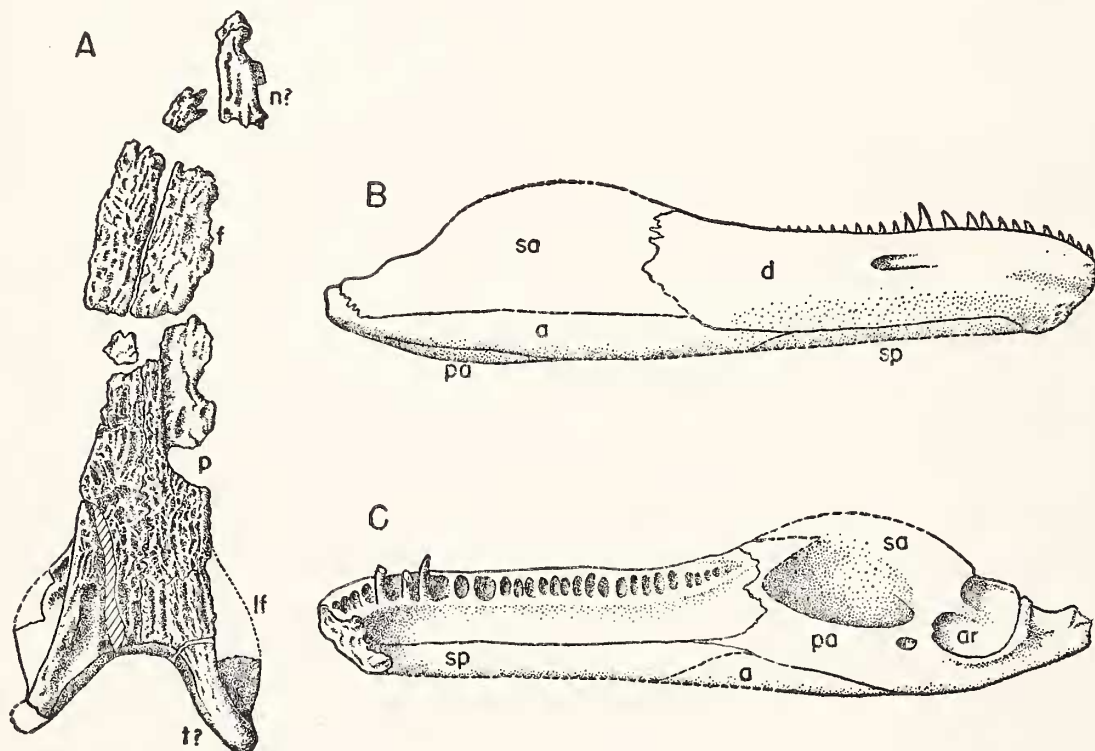


FIG. 8. *Megamolgophis agostinii*. A, remains of skull roof; the outlines of the shelf lateral to the skull table are restored. B, C, attempted restoration of the jaw, outer and inner views. The length in the region of angular and surangular is uncertain. No. 8614. Abbreviations: a, angular; ar, articular; d, dentary; f, frontal; lf, lateral flange; n, nasal; p, parietal; pa, pre-articular; sa, surangular; sp, splenial; t, tabular. $\times 1/2$.

The skull roof materials include, anteriorly, a pair of elements, each about 30 mm. in length and 10 mm. in breadth, which are reasonably identified as frontals; anterior to them are fragments which may represent nasals. Posterior to the presumed frontals is an elongate mass of sculptured bone clearly traversed for most of its length by a zig-zag median longitudinal suture. I interpret the major part of this structure as consisting of a pair of elongate parietals. A tiny pit may possibly be a parietal foramen. Posteriorly, the sculptured surface ceases abruptly at a vertical flange, presumably the upper margin of the occipital surface; on either side of the mid-line, the posterior margin curves backward to terminate in a pointed projection comparable to a labyrinthodont tabular "horn." Sutures are not clear in the posterior portion of this skull table. The sculpture pattern suggests that this region contained a series of postparietal elements. It is reasonable to assume that tabular elements constitute the pair of "horns." Whether the median part of the posterior margin included a pair of postparietals in the more usual pattern of Paleozoic amphibians or a single element, as in *Lysorophus*, is uncertain. I could find no clear sutures on the occipital aspect.

Anterior to the "horns," the lateral margins of the skull roof mass are, as far as preserved, distinct and nearly straight, obviously without any close sutural union in life with adjacent elements. A unique feature is the development on either side of a broad flange of bone extending outward from the table at a level considerably below the sculptured surface. This flange commences posteriorly at the tabular "horn," becomes at once prominent, and runs forward to about mid-length of the parietals. It is not completely preserved on either side, but the parts remaining enable one to restore its outlines, as in the figure, with some confidence.

This skull roof differs notably from that of *Lysorophus* in two features: the sculpture and the sharp occipital boundary. It is, of course, possible that its association with the other material is accidental and that it does not belong to the genus here described. But such an assumption does not greatly help the situation. Apart from a resemblance to *Ophiderpeton* (cf. Steen 1931: pl. V, fig. 2), a form quite unknown in the Permian, this skull roof does not resemble that of any other known amphibian. However, the presence of sculpture, in contrast with the *Lysorophus* condition, may perhaps be correlated with increased size, and the skull appears to have been of proportions appropriate to the jaw material described below. Further, the most

peculiar feature, the free lateral margin of the table and the underlying flange, is readily interpretable by reference to *Lysorophus*. In that animal the cheek region consists only of the elements of the jaw suspensorium, the upper element of which — variously termed “supratemporal” or “squamosal” — was braced against the side of the table. The prominent elongate groove formed here between the flange and the overlying table margin would have been a most effective bracing device to receive the broad head of the “supratemporal.”

Some of the bone on the under surface of the mass which includes the roofing bones is not interpretable. Anteriorly, however, there are incomplete remains of a bone which appears to be a maxilla. A series of alveoli and a few teeth can be made out along the presumed lower margin. Half-way along the portion preserved, the bone is greatly thickened and appears to have carried, here, two or three exceptionally large teeth — the development of a “canine” region, seen in various Permian amphibians and reptiles. Above this thickened area is a dorsal extension of the maxilla, somewhat fan-shaped as preserved, and roughly comparable to processes seen in the “canine” region in pelycosaurs (for example).

Lower jaw material (fig. 8B, C) is present in both major specimens. No. 8583 includes the posterior three-fifths of the right dentary and two fragments (including the symphyseal region) of the left. No. 8614 includes, in three pieces, what appears to be a nearly complete right ramus, but this is badly disarticulated, crushed and eroded. Between the two specimens the dentary is nearly completely known. (The bone in no. 8583 appears at first glance to be larger but the seeming discrepancy is, in the main, due to differences in preservation.) The dentary composed most, if not all, of the symphysis. The outer surface is smooth, without sculpture; at about half length there is a large mental foramen. Posterodorsally, zig-zag rugosities suggest an overlapping suture with the surangular externally; the posterior border is incomplete. There is a vertical inner surface which gives no indication of the presence of coronoids. The external and internal lamina of the dentary are widely separated ventrally, indicating the presence in life of a splenial or splenials to complete the ventral aspect of the jaw ramus. About 30 teeth are present in a distance of approximately 80 mm. At their bases the teeth appear to have been essentially circular in section; toward the apices the few that are well preserved are mediolaterally compressed.

The posterior portion of the jaw is present only in no. 8614. There is a deeply incised articular surface, divided into two portions. This is broadly exposed on the inner surface if (as in the figure) the jaw is laid flat on its outer side; presumably in life it lay in an essentially horizontal plane, the jaw sloping strongly inward ventrally. There is a very highly developed retroarticular process.

A mass of badly crushed and broken bone appears to include the intermediate region of the jaw. I have restored this region, but am none too sure of the structure here, or of its extent; the jaw may have been one to three centimeters longer than figured. The outer surface appears to show a low angular and a more highly developed surangular. On the presumed medial surface a flat bone with a curved margin appears to be a prearticular bounding a typical Meckelian fossa.

Despite many unfortunate gaps in our knowledge, it is obvious that this large snake-like amphibian is a new and very distinctive type, readily distinguishable in various features from even such a related form as *Lysorophus*. It may be formally designated as *Megamolgophis agostinii*, gen. et sp. nov., with combined generic and specific characters as follows: a large lysorophid in which the longitudinal ridge-system of the vertebral centra is more complex than in other known genera — the ventral ridge at the least distinctly double, regionally a development of a considerable series of closely appressed lamellae covering the entire external surface of that element; dermal roofing bones of the skull sculptured; dentary with approximately 30 teeth. Holotype of *M. agostinii*, no. 8583, is from locality 28. The specific name is in honor of Mr. Charles Agostini, preparator on the Carnegie Museum staff who took a major part in the work of collecting the Dunkard material.

Desmatodon hollandi

This genus and species of reptile was founded on a jaw fragment from locality C in the Conemaugh (Case 1908: 236-237, figs. 4, 5C, pl. 59, fig. 1; no. 1938). Four teeth are present and the root of a fifth. As Case noted, the cuspidate teeth resemble those of the Permian cotylosaur *Diadectes*, but are rather more primitive in nature. Since cuspidate teeth are present in several other groups of Permo-Carboniferous reptiles, the present writer had not felt certain, on the basis of existing figures and description, that this form was a diadectid. However, study of the original material and comparison with teeth of *Diadectes* fully justifies Case's conclusion. The tooth figured by Case is the least developed of the four present; the other members of the

series are rather more clearly diadectid in character (pl. 1, fig. 3).

Diadectid "molar" teeth show a pattern reversed in upper and lower jaws; in the upper teeth the major cusp is lateral in position, in the lower teeth, medial. Since Case refers to the major cusp in *Desmatodon* as lateral, it is obvious that he considered the specimen as pertaining to the upper jaw. Although this is uncertain (not improbably the specimen is the anterior portion of the tooth battery of the left dentary), we retain his orientation. In *Diadectes* the inner portion of an upper tooth is greatly expanded, and a secondary cusp is there developed, between which and the primary cusp a wearing surface arises (fig. 9). In *Desmatodon* the secondary cusp is not present as

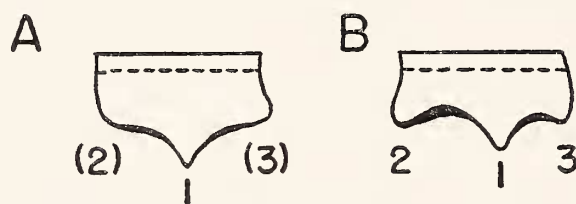


FIG. 9. Outlines of "molar" teeth in anterior view, outer margin to right; in *A*, *Desmatodon*, and *B*, *Diadectes*, to show cusp development. 1, 2, 3=primary, secondary and tertiary cusps of *Diadectes*; (2), (3)=incipient cusps of *Desmatodon*; thickened lines=areas of wear.

such, but there is a highly developed medial swelling (more pronounced on other teeth than on that illustrated by Case) and in two of the four teeth there is here a small area of wear. In *Diadectes* upper "molars" there is also present a tertiary lateral cusp and a smaller, secondary area of wear between it and the principal cusp. In *Desmatodon* this region is somewhat developed although lacking a formed cusp, and one of the four teeth shows wear here. The *Desmatodon* teeth thus appear to be built on the fundamental *Diadectes* pattern, but are far more archaic than in *Diadectes*; the most highly developed *Desmatodon* teeth are comparable to the least developed molars of *Diadectes*—those at the front or back ends of the "molar" batteries. *Desmatodon* may well be, as its stratigraphic position suggests, a direct ancestor of *Diadectes*. Measurement of the linear spacing of the teeth in the *Desmatodon* type gives a figure which is the same as that seen in a specimen of *Diadectes* in the Harvard collections (no. 1743) from a low horizon in the Wichita group of Texas. This specimen is unusually small for a member of that genus and has but about three-fourths the linear dimensions of such an individual as the mounted specimen in the American Museum of Natural History (Case 1910, fig. 5). Small size might reasonably be expected if *Desmatodon* is an ancestral form.

It is possible that a few fragments of bones of diadectid appearance from the vertebrate bonebed at Danville, Illinois, and of the same general late Pennsylvanian age may pertain to *Desmatodon*.

Case suggested that certain other remains from Pitcairn were also of diadectid nature. As noted elsewhere, they are, however, probably amphibian.

I note here a specimen, likewise from the Conemaugh (locality 1), which consists of a series of "cheek" teeth, possibly of the left dentary, of a tiny and seemingly primitive diadectid (no. 8567, pl. 1, fig. 4). They form a battery of transversely elongated teeth set in an oval bony rim similar to that which in *Diadectes* surrounds the cheek tooth series. Five teeth are well preserved, except for their tips; stumps of three others are present; the total battery of cheek teeth appears to have consisted of 8 members, contained in a length of 11 mm. The nature of the tooth arrangement together with their transverse elongation strongly indicates that these teeth pertain to a diadectid. There is, however, but a single sharp cusp on each tooth, this at the presumed outer margin. The specimen was contained in obverse and reverse slabs of shaly limestone; the cusp tips had been broken off when the piece was split, and embedded in the reverse slab. By careful preparation one of these tips was freed and glued in position. The cusp tips were turned sharply outward; externally, the tooth falls vertically from the cusp tip to tooth base and shows a worn surface. An arched ridge curves medially along the tooth from the cusp tip to descend at the inner extremity of each tooth. On three of the teeth there appears to be evidence of wear part way along this ridge.

This tooth pattern, with but a single cusp and no cusp or "shoulder" lateral to it, is more primitive than in any described diadectid. It is possible that this fragment represents a small and primitive diadectid otherwise unknown. I hesitate, however, to formally describe it on the basis of this single specimen. Further, it is not impossible that it pertains to a young *Desmatodon* with some sort of "milk dentition." The teeth in this specimen can be compared to the "summit" portions of *Desmatodon* teeth, with the basal region undeveloped. Provisionally I assign the specimen, with considerable doubt, to that form.

"*Pareiasauroides*"

A cast-like structure found at locality E in the Conemaugh formation was referred to Case (1917), who compared its general proportions with those of the radii of pareiasaurs of the South African Permian but did

not further commit himself. White (1917) designated it as *Pareiasaurus ? henneni* (a name later changed to *Pareiasauroides henneni* Lull 1924). This terminology is unwarranted, for there is no evidence that this specimen is of organic nature; and very certainly it is no pareiasaur (Romer 1935: 1635).

***Limnosceloides dunkardensis* gen. et sp. nov.**

The U. S. National Museum collections contain a partial skeleton of a cotylosaur of moderate size (no. 12166) which was collected by Boyd C. Baker five miles southwest of Cottageville, Jackson Co., West Virginia. This area lies in the Dunkard group, but the horizon is uncertain. Except for a fragment which may possibly include a broken section of an oval tooth, all identifiable elements are from the posterior part of the body, the material including vertebrae, pelvic fragments, and much of the hind legs (figs. 10-12).

Of vertebrae, there is a centrum which may be from the anterior dorsal region. There are, further, 16 vertebrae from the posterior portion of the column. These include: a series of four articulated lumbar; a fifth lumbar which may have been next in succession; a first sacral which was articulated with the last mentioned; five proximal caudals which are not articulated with the sacral; remains of five distal caudals. The upper portions of most of the vertebrae have been weathered off, in most cases shortly above the level of the zygapophyses. Intercentra of small size appear to have been present in the lumbar and proximal caudals and are preserved in three instances; the base of a chevron is seen between one pair of distal caudals.

The vertebrae are characteristically cotylosaurian, and except for size are, for the most part, not readily distinguishable from those of *Limnoscelis* and *Labidosaurus*. Although the neural spines are missing in the lumbar vertebrae, enough of the arches are present to show their "swollen" nature, with zygapophyses placed far out laterally, the zygapophysial surfaces in a horizontal plane and marked with concentric lines. The lumbar show rib facets, diminishing in size posteriorly, at the base of each neural arch, below the projecting buttress of the anterior zygapophyses; the first sacral has a two-faced articular surface of enormous size, on the arch and the adjacent region of the centrum, for a sacral rib. In the proximal caudals, bases of ribs are preserved, attached to the vertebrae. The ribs have conjoined heads articulating with a short transverse process of the neural arch and with a raised area, below and in front of this point, on the

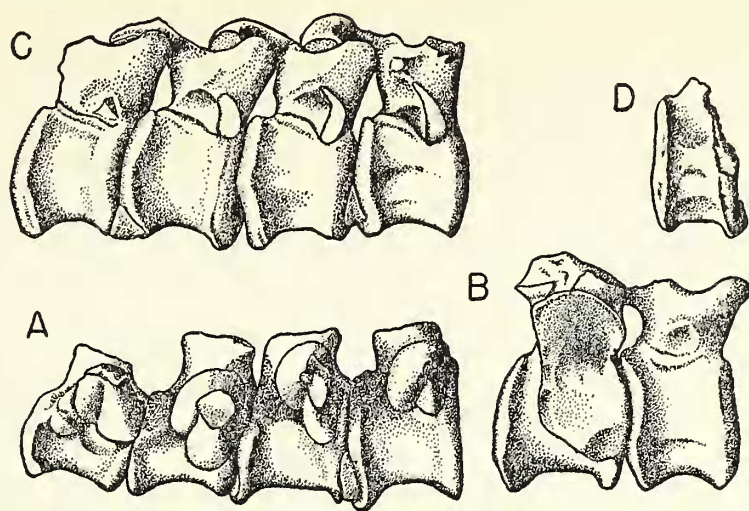


FIG. 10. Vertebrae of *Limnosceloides*, seen from the right side. *A*, proximal caudals; *B*, first sacral and last lumbar; *C*, series of lumbar and posterior dorsals; *D*, incomplete anterior dorsal. $\times 1/2$.

centrum. It is obvious that the small lumbar ribs and the large first sacral rib were not fused with their vertebrae; in the proximal caudals, the tuberculum is fused with the arch, but the capitulum is apparently suturally separate from the centrum. In the lumbar, neural arch and centrum are suturally distinct; in the sacral and caudals, fusion has occurred.

Measurements of the centra are as follows, the two measurements (in mm.) given for each element being lengths taken along the lateral surface and widths across the posterior edge: dorsal, 16, 26; presacral 5, 19, 23; presacral 4, 18, 24; presacral 3, 19, 24; presacral 2, 19, 25; presacral 1, 19, 25; sacral 1, 21, 26; caudal 1 (?), 19, 24; caudal 2 (?), 18, 21; caudal 3(?), 18, 21; caudal 4(?), 18, 20. Of the pelvis, the pubis and part of the acetabular region are preserved on the left side; the latter region is well preserved on the right. Unfortunately, the iliac blade,

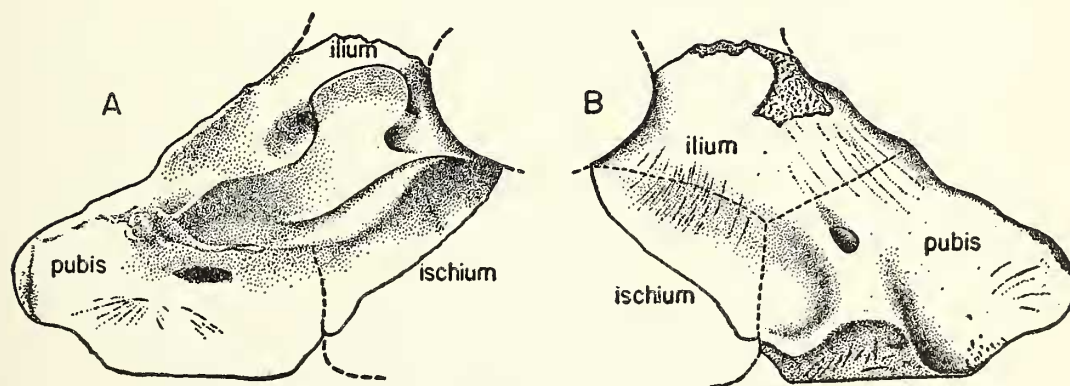


FIG. 11. *Limnosceloides*, incomplete pelvis, external and internal views of left side (partially restored from right). $\times 1/2$.

potentially diagnostic, is not preserved. The construction is that of a captorhinomorph. The pubis is built in a fashion comparable to that in *Labidosaurus* and *Limnoscelis*. As in both these genera, the pubis has a thickened dorsal forward projection, below which the margin of the bone retreats posteromedially toward the symphysis. The pubis in proper articulation turns broadly outward dorsally, so that the external surface in life faces as much ventrally as laterally; the dorsal surface (for pubo-ischio-femoralis internus) does not, however, face as much anteriorly as in diadectids or typical rhachitomes. As in *Labidosaurus* and *Limnoscelis*, the major area of the pubic symphysis lies at the lower end of a thickened internal ridge and is sharply demarcated from thinner symphyseal regions lying more anteriorly and posteriorly. The inner opening of the obturator foramen pierces the upper end of this thickened ridge, rather than lying anterior to it as in *Labidosaurus*.

The right femur is preserved, but is somewhat crushed and imperfect distally, and the crest which bore the internal and fourth trochanters has been broken off; the length can be estimated as very close to 100 mm. A fragment of the proximal end of the left femur is also preserved. The bone exhibits general cotylosaurian and captorhinomorph features and in correlation with the animal's size is stockily built. It is obvious that the missing trochanteric crest was very strongly developed, but the contours of its base indicate that it did not flare widely anteriorly as do those of both *Labidosaurus* and *Limnoscelis*. The distal portion of the ventral ridge system is low but sharply defined and slants posteriorly to the posteroventral margin of the posterior condyle; the ridge is paralleled anteriorly by a longitudinal groove. Although the bone is imperfect distally, its contours make it improbable that the excavation of the side of the posterior condyle, prominent in both *Labidosaurus* and *Limnoscelis*, was developed to any degree here. The ventral popliteal surface is deeply excavated adjacent to the anterior condyle. On the head of the bone a distinct ridge is developed dorsally from the area which I believe to have carried the pubo-ischio-femoralis internus attachment. Both the femur and tibia are incompletely ossified at the ends; whether this is a feature of the species or indicates a juvenile condition cannot, of course, be said. The right tibia is nearly complete, with a length of 72 mm., but is somewhat weathered and crushed; the head of the left tibia is present in a better state of preservation. The bone does not differ notably from the sturdy tibiae of other cotylosaurs. The ridge

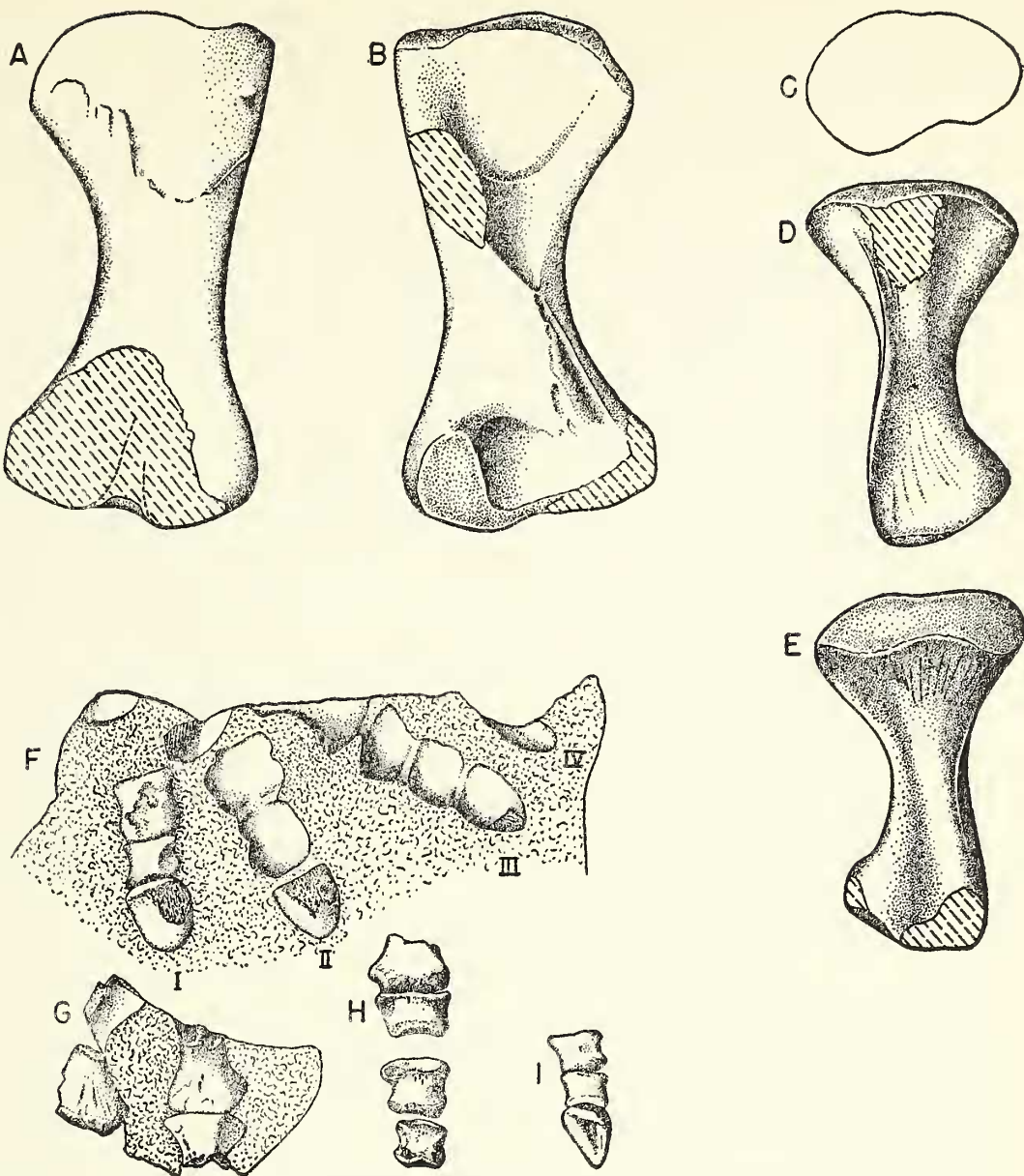


FIG. 12. *Limnosceloides*. A, B, femur in dorsal and ventral views. C-E, tibia, outline of proximal end, extensor surface and flexor surface. F-I, material of pes. F, part of left foot, in sandstone block; part represented by impressions only. G, ventral surface of two metatarsals and a phalanx of right foot (?) in small sandstone block. H, articulated end of metatarsal and two further non-associated phalanges of right foot (?). I, articulated phalanges of (?) fifth digit. $\times 1/2$.

separating extensor and flexor surfaces medially is sharply developed and extends well proximally, medial to the cnemial crest.

Considerable portions of the left pes are preserved as impressions or weathered bone in a sandstone slab, and a number of other fragments most, at least, from the right foot, are also present (fig. 12 F-I). These suggest a typical cotylosaur foot, nearly as stoutly built as that of *Limnoscelis*.

As seen from the above description, we are dealing with a captorhino-

morph cotylosaur intermediate in size between *Labidosaurus* and *Limnoscelis*, the latter being the largest member of the group known at present. In general the linear measurements of this animal are about half again as great as those of *Labidosaurus* of Texas; *Limnoscelis*, again was about 50 per cent larger than the present form which (assuming the usual presence of a long tail) might have had a total length of about 145 cm., or somewhat under 5 feet. The build was obviously of the heavy type — with short but stout limbs — expected in a cotylosaur of this size.

It is clear that this skeleton is that of an animal unknown in the roughly contemporaneous deposits of the southwestern Redbeds and, despite the unfortunate lack of knowledge of cranial structure, merits a name for purposes of reference. It may be termed *Limnosceloides dunkardensis*, gen. et sp. nov., a captorhinomorph cotylosaur with combined generic and specific diagnoses based on the character of the femur, in which the antero-proximal trochanteric crest is not extended anteriorly and the distal part of the ventral ridge system is a distinct, if low, crest running diagonally distally to the outer ventral margin of the posterior condyle. The genus may be (very tentatively) assigned to the Limnoscelidae.

***Melanothyris morani*, gen. et sp. nov.**

One of the earliest discoveries of the Pittsburgh parties in the Dunkard was at locality 9, near Blacksville, West Virginia, where numerous small bones and more or less complete skulls and jaws were found in nodules of impure limestone. The material is worthy of careful preparation, but requires more working time than is at the moment available. Most if not all the remains are those of a small cotylosaur. Pending further preparation and study, this may be formally described as *Melanothyris morani*, gen. et sp. nov.; combined generic and specific characters: a captorhinomorph cotylosaur with but a single row of teeth in upper and lower jaws, comparable as far as known to *Romeria* in many regards, but possessing only four pre-maxillary teeth, of which the first two are enlarged, and with "canines" developed at the anterior end of the maxilla, rather than in the more posterior position seen in most primitive reptiles. Genoholotype, no. 8617, from locality 9. The specific name is in honor of Mr. William E. Moran, who discovered the Blacksville locality and participated in all the expeditions on which the material discussed in this paper was collected.

Among the specimens from locality 6 are some seven showing the remains of small upper and lower jaws (no. 8566), seemingly of reptilian nature and possibly belonging to the Blacksville reptile, as suggested by size, contours and nature of the dentitions.

Edaphosaurus raymondi

The grotesque pelycosaur *Edaphosaurus* [*Naosaurus*], ornamented with long neural spines bearing cross-bars, is the one common reptile in the collections. This is not unexpected, for the genus has long been known from late Carboniferous and early Permian deposits in a variety of American and European areas and was apparently ubiquitous in those continents in late Paleozoic times. In this area its remains range vertically from the Conemaugh to the high levels of the Dunkard. Generic identification is, of course, rendered easy through the characteristic development of the spines, of which even a small segment is readily recognizable.

In Texas, *Edaphosaurus* is not in general a conspicuous member of the fauna; its remains are common only in two bonebeds of unusual type which appear to represent swamps; it appears to have been, in all probability, a feeder on the lush vegetation of such areas,¹ and hence is relatively rare in deposits presumably yielding faunas of relatively dry terrestrial areas. The relative abundance of *Edaphosaurus* in the present collections suggests that this was a region which was persistently of a wetter, more swampy type than was the Texas "delta."

Edaphosaurus raymondi was described by Case (1908: 237-238, fig. 7; pl. 59, fig. 3) on the basis of a short segment of spine (no. 1941) from locality C in the Conemaugh group. The spine exhibits the lateral tuberculations characteristic of "*Naosaurus*" (= *Edaphosaurus*) and was tentatively assigned by Case to that genus. This appears eminently reasonable; such tuberculations are unknown in any other form. The spine is much too small for any of the better known American species, and the horizon is a much earlier one. But, *Edaphosaurus mirabilis* (Fritsch) of Bohemia is likewise small and likewise early in appearance (cf. Romer and Price 1940: 388).

Edaphosaurus* cf. *boanerges

In the Washington group and the lowest part of the Greene there have been found at a number of localities fragmentary remains of an *Edaphosaurus* of moderate size, comparable, as far as can be deter-

¹ cf. Romer and Price 1940: 175-176, 387, 390.

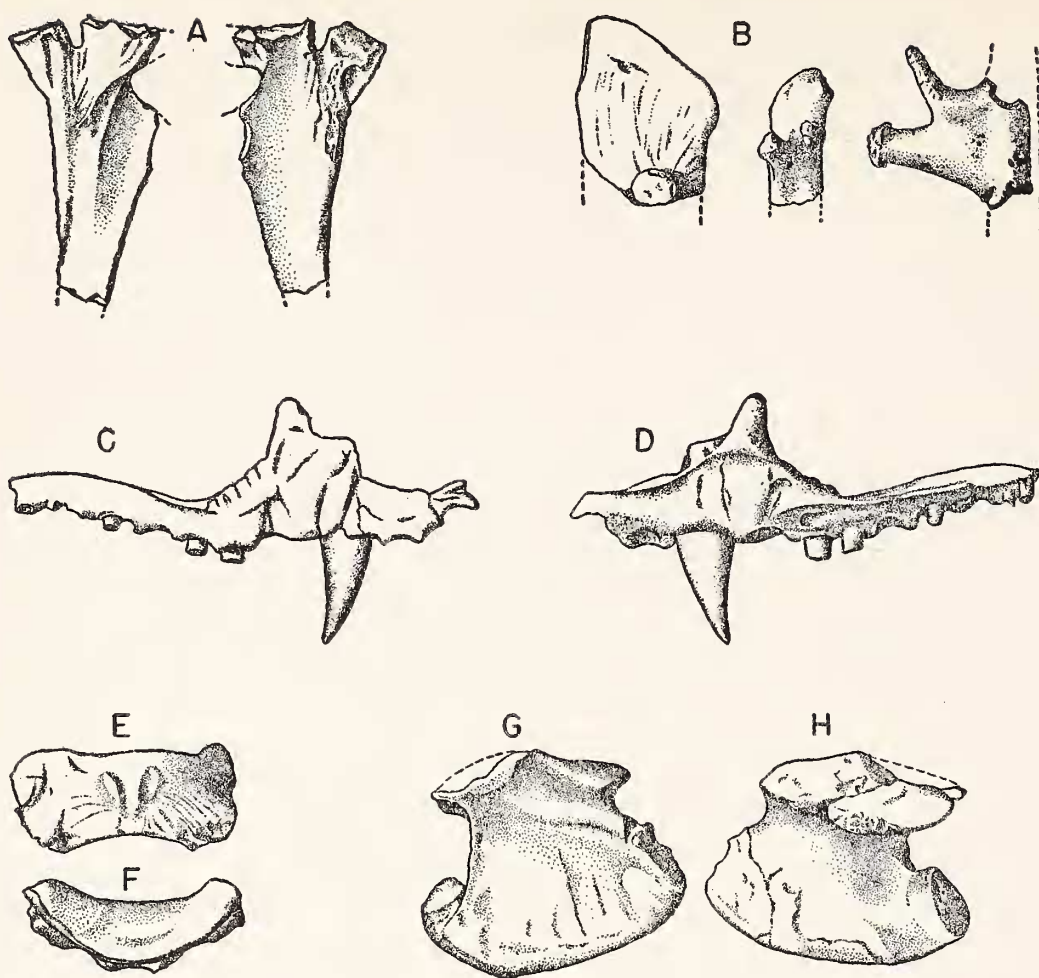


FIG. 13. Pelycosaur remains. *A*, (?) axis rib of *Edaphosaurus*?, no. 8579; *B*, spine fragments of *Edaphosaurus* cf. *cruciger*, no. 8540; *C*, *D*, external and internal views of right maxilla of *Baldwinosaurus*? *dunkardensis*, no. 8563; *E*, *F*, ventral and anterior views of an intercentrum, presumably the atlantal, of a large ophiacodont, no. 8577; *G*, *H*, external and internal views of a sacral rib of ophiacodont type, no. 8576. *A-F*, $\times 1/2$; *G, H*, $\times 1$.

mined, to *E. boanerges* of the Admiral formation (Wichita group) of Texas. These include, in the present collections, spine fragments from localities 8 and 12; an ilium, partial humerus, metapodial and spine fragment from locality 6; also from that locality a puzzling specimen (fig. 13A, no. 8579) which has much the appearance of a crushed pelycosaur stapes but is very probably an axis rib of *Edaphosaurus*; Tilton (1930: 111) reported a spine fragment from locality G; further spine fragments occur at locality H (Stauffer 1916: 88; Stauffer and Schroyer 1920: 147, figs. 45, 46; Whipple and Case 1930: 370); and fragments of spines and ribs are reported from locality I (Whipple and Case 1930: 370-372)¹.

¹ This material was compared by Case to *E. cruciger* of Texas, a species which at that time included the material of the related *E. boanerges*.

Edaphosaurus* cf. *cruciger

E. cruciger of Texas is closely related to *E. boanerges*, but appears to be a descendant characteristic of a higher level in the Wichita group; it is of somewhat larger size and has a greater development of lateral projections and an expansion of the tips of the cervical spines not found in *E. boanerges*. The several citations of *Edaphosaurus* from the upper portion of the Greene group are tentatively assigned to this species since they appear to be from a larger form than that of the Washington group and since the last of the finds noted below shows characters definitely suggestive of *E. cruciger*. These finds include spine fragments from locality 25, spine and rib fragments from locality 28, spine and rib fragments and a clavicle from locality 37, and from locality 35, scraps of vertebrae, spines and ribs and a partial tooth plate. The fragments from the last locality include the tips of two cervical spines (fig. 13B). These show distally a modest expansion comparable to that of *E. cruciger*; as far as is known, no such expansion was present in material (of *E. boanerges*) from the earlier Wichita. There is in this specimen a tendency, apparently, to an exuberant development of lateral growths; a fragment of spine shaft shows a double process at one point, and the smaller tip exhibits a cluster of processes springing from a common base.

***Baldwinonius* ? *dunkardensis* sp. nov.**

A pelycosaurian jaw fragment of uncommon type, from locality 6, is that shown in figure 13 C, D. This consists of the greater part of a right maxillary, from which most of the thin portion lying on the side of the face has been lost but leaving most of the tooth-bearing margin and the thickened area containing the "canine" sockets. Anteriorly, the bone is apparently complete to the premaxillary articulation. Behind this point is a short region which is toothless and with a slight downward "step." There follows an alveolus for a tooth of modest size; behind this a pair of enlarged "canines," one of which is present, the other represented by a large socket. Behind this point there is a sharp reduction in tooth size. The ramus is incomplete posteriorly; the portion preserved contains seven teeth, broken at their bases, or alveoli. The only well-preserved tooth is the "canine." This is pointed and slightly recurved. It is essentially rectangular in section basally and although becoming sharper distally, does not (in contrast to spenacodonts) develop sharp anterior or posterior margins. As far as can be seen, the post-canines are subquadrate at their bases.

Markings on the outer surface appear to be post-mortem checks or cracks. The posterior portion exhibits on the internal aspect a medially-facing surface for apposition to the palatine, above which an upward-facing shelf overlies the tooth sockets. More anteriorly there is a swelling containing the "canine" sockets, which has a thickness of about half its greatest height. A groove, presumably for bloodvessels, crosses the upper margin of this swelling, somewhat as in sphenacodonts. Above this point the swelling rapidly subsides; there is, however, a continuation upward of a finger-shaped thickening of the maxillary bone in somewhat the fashion of the ophiacodonts—a feature responsible for the preservation of this region of the maxilla.

This bone is that of a pelycosaur not readily comparable with any common redbeds type. The enlarged canines, combined with other features which are ophiacodontoid in character, suggest a reference to the (possibly artificial) assemblage of tusked ophiacodontoids which I have termed the Eothyrididae. Most closely comparable is the incompletely known *Baldwinonus trux* of New Mexico (Romer and Price 1940: 255-257). The present specimen differs, however, in that there is but a single pre-"canine" maxillary tooth, and in that the supra-"canine" swelling is less developed dorsally. These characters may be considered as defining a new species referred, with some doubt, to *Baldwinonus*, with no. 8563 as the holotype.

Undetermined Pelycosaur Remains

A few fragmentary specimens from the Dunkard appear to be remains of pelycosaurs of types unknown in the Permian of other regions, but not in themselves worthy of taxonomic description.

(1) From locality 6, a right sacral rib of an ophiacodontoid (no. 8576, fig. 13 G, H). The broad blade of the rib measures 24 mm. in anteroposterior length, and is thus about one-third the dimensions of that of *Ophiacodon retroversus*. Its short, expanded shape and the pronounced swelling at its posterior border indicate its pertinence to an *Ophiacodon*-like animal (cf. Romer and Price 1940: fig. 45A, B). It is seemingly too small to belong to the form described above as *Baldwinonus dunkardensis*.

(2) A large intercentrum, also from locality 6 (no. 8577, fig. 13 E, F). This measures 39 mm. from tip to tip and 16 mm. anteroposteriorly along the midline. It is obviously reptilian, rather than amphibian, and belongs to a reptile of very large size, in which the diameter of the corresponding centrum was on the order of 50 mm. This is a size

reached or approached by few known American Permian reptiles: the pelycosaurs *Ophiacodon major*, *Dimetrodon grandis*, *Cotylorhynchus romeri* and (somewhat smaller and earlier) *Stereophallodon ciscoensis*. The general proportions and the deeply-cupped and smoothly-rounded anterior face strongly suggest that this intercentrum was in the atlantal position, forming part of the articulation with the occipital condyle, and the facets for the articulation of the rib head also suggest this position. If atlantal, this intercentrum differs markedly from that of *Dimetrodon*. This element is not described in *Cotylorhynchus* and is unknown in *Stereophallodon*. The specimen differs in detail from the atlantal intercentrum of *Ophiacodon*, particularly in the presence of paired tuberosities on the ventral surface, but resembles it in general proportions. Not improbably it pertains to a large ophiacodontoid of some type, but one larger than *Baldwinonius? dunkardensis*.

(3) At locality 33 was found a fragment of a bone V-shaped in section which resembles the base of the sphenoidal rostrum of a pelycosaur (no. 8574). The form possessing it must have been of considerable size but the fragment is too imperfect to permit of satisfactory identification.

Indeterminate Reptilian (?) Remains

As noted in Moran's accompanying paper (under locality D), Condit (1912: 28, 39, 283) reported reptilian bones from the Ewing limestone and Birmingham shale of the Conemaugh of Ohio; these bones, however, were not preserved (Case 1915: 84) and are hence indeterminate.

Footprints

Footprints of tetrapods have been discovered in a number of localities in the late Pennsylvanian and in the Dunkard of this region. They are currently being studied by Mr. Donald Baird, and I shall here merely review briefly those published.

Tilton in 1926 (386-391, pl. 11, figs. A-E) described a number of footprints from West Union, Doddridge Co., West Virginia, in the Waynesburg sandstone of the Washington formation; these he named *Baropus waynesburgensis* (1931: 551-555, figs. 3, 4). They are broad, stub-toed tracks which, as Gilmore pointed out, are similar to those described from the late Carboniferous and early Permian of other regions as *Allopus* (cf. Gilmore 1926: 30), and appear to pertain to rhachitomous amphibians. The West Virginia animal was one of good size; length and breadth of a forefoot track is 115 mm., thus not inappropriate for an animal of about the size of a typical *Eryops* of

the Wichita of Texas (cf. the forefoot of *Eryops* as described by Gregory, Miner, and Noble 1923).

Carman (1927: 386-388, pl. 2) described a slab of footprints from a horizon just below the Benwood limestone member of the Monongahela formation from Center Township, Morgan Co., Ohio.¹ These constitute a trackway with a breadth of about 250 mm. and a stride of 540 mm.

Tilton further described from the sandstone of the lower Dunkard from Berea, Ritchie Co., West Virginia, a pair of tracks of distinctly reptilian type (1931: 547-551, figs. 1, 2). He notes that they are of a sort which might have been made by *Dimetrodon* or a related pelycosaur. This is possible, but an even closer comparison can be made with *Edaphosaurus*. Tilton gave the name *Dimetrodon berea* to these prints; they were renamed *Dimetropus* by Romer and Price (1940: 336).

Happ and Alexander (1934) described several types of small footprints from the Dunkard — presumably the horizon of the Marietta sandstone — at Sherman, West Virginia.

Coprolites

In various early Permian deposits, and to a lesser degree in those of late Pennsylvanian age, are found numerous animal faeces in the form of coprolites. These are particularly abundant in the Texas Redbeds. Striking and abundant are slender, elongate, cigar-shaped specimens which show a spiral surface marking at one end. These were obviously excreted by forms with a spiral valve type of intestinal structure. Such an intestine is known to have been present in the "pleuracanth" sharks which were ubiquitous inhabitants of late Paleozoic fresh waters, and it is probable that the greater part, at least, of such coprolites are of "pleuracanth" origin. However, a spiral valve is present in lungfishes, and there is some possibility that Paleozoic crossopterygians and perhaps even some of the more primitive actinopterygians and the more primitive amphibians may have retained such a structure. In consequence we cannot be sure that all coprolites of spiral type are of "pleuracanth" origin.

Abundant coprolites of this type have been described by Price (1927: 214-225, pls. 11-18; Price, Tucker and Haught 1938: 157) from the Round Knob formation (Pittsburgh shale) of the Conemaugh from the

¹ Carman further described other amphibian footprints from an earlier horizon (Allegheny formation) not considered here.

Morgantown region of West Virginia, and Stauffer and Schroyer (1920: 146, 147, figs. 30-35, 41-44) have described other specimens from the Elm Grove limestone and Creston Redbeds of the Washington formation at Raven Rocks and Elba, Ohio, respectively.

Less commonly collected in the Texas Redbeds are coprolites lacking the spiral structure and taking the general form of oval, flattened, and rather amorphous masses. Presumably such coprolites were generally of amphibian and reptilian derivation. Their rareness in collections is due in part to their scarcity in the deposits, but also due to the fact that the collector is less liable to recognize them as of "organic derivation." Tilton (1926: 388, 394) has reported such coprolites from the Ninevah and Lower Rockport limestones of the Greene group of the Dunkard.

In the present material, coprolites were collected at localities 18, 20 and 26, and were found but not collected at a number of other localities.

DISCUSSION

The present collection is, as noted earlier, of interest in two regards: (1) the Dunkard material, constituting its bulk, gives us an opportunity to study the early Permian vertebrate fauna of a region both topographically and, it seems, environmentally as well, far removed from the classic Redbeds of the American Southwest; (2) the late Pennsylvanian materials give us a glimpse of vertebrate faunas transitional between those of the typical Coal Measures and those of the Permian.

Occurrences of vertebrates in the late Paleozoic of the region here discussed are listed by localities, stratigraphically arranged, in the accompanying table. Most of these localities (from number 4 on) lie in the Dunkard, and represent a broad spread of horizons covering nearly the whole extent of the Washington and Greene groups which constitute that series.

The exact correlation of the Dunkard with the Texas beds is open to some question. Although the Washington flora has a Pennsylvanian aspect, the base of the Dunkard is generally considered to be the base of the Permian in this region, and the base of the Wichita Group of Texas is held to be at this same horizon. Hence, part and perhaps all of the Dunkard can be correlated with the fossiliferous Texas beds. In the latter state, the vertebrate faunas continue upward, with gradual change, into the Clear Fork group. Does any part of the

Dunkard extend this far up the column? No positive answer can be given, but there is some suggestive evidence in the negative. *Edaphosaurus* is represented in both areas. In Texas, *E. boanerges* appears to be the lower to middle Wichita species, *E. cruciger* that of the upper Wichita and *E. pogonias* the Clear Fork form. The three apparently form a species phylum, the later forms being successively larger and with increasing "exuberance" of spine development. As noted earlier, the Dunkard *Edaphosaurus* material from the Washington and lower Greene appears comparable to *E. boanerges*, that from upper levels of the Greene to *E. cruciger*; none exhibits characteristics of *E. pogonias*. We may reasonably conclude that the Dunkard, as a whole, is essentially comparable to the Wichita group of Texas and compare the faunas on that basis.

Both Dunkard and Wichita collections contain fairly abundant freshwater fish remains, and the content is very similar in the two. Both yield plentiful *Dittodus* teeth and (more rarely) spine and cartilage material of this "pleuracanth" shark type; both have abundant remains of the lungfish *Sagenodus*; both have remains (usually not well-preserved) of palaeoniscoids; a crossopterygian — presumably *Ectosteorhachis* in both cases — is present but not common. It is possible that differences of at least specific nature may eventually be discovered, but at present this is not the case.

In the amphibian fauna, the common large labyrinthodont in both areas is the familiar *Eryops*. The common Texas Wichita labyrinthodont of smaller size is *Trimerorhachis*. This cannot be identified with certainty in the Dunkard, but we have noted the presence, in a number of localities, of fragmentary remains of rhachitomes of roughly comparable size and of seemingly similar character. *Lysorophus*, present in the Dunkard, is not recorded in the Wichita; but since the genus had developed before the end of the Carboniferous and is present in Texas in the later Clear Fork beds, it may yet be found in the Wichita. "Horned" nectridians are present in both regions, although the Texas form, *Diplocaulus*, is relatively rare in Wichita horizons.

These resemblances between the Dunkard and Wichita amphibian faunas are balanced by marked differences. Various Wichita forms are absent in the Dunkard material. In the case of certain rare types, seeming absence may be due to chance. There are, however, two common Texas types which, if present in the region, would have been

expected in Dunkard collections; these are the aquatic embolomere *Archeria* [*Cricotus*], whose characteristic centra are readily preserved and easily recognized, and the terrestrial rhachitomes of the dissorophid group. No trace of either has been so far discovered in the Dunkard. As was said above, long-horned nectridians are common in both the Texas and Dunkard beds. But, although I at first assumed that the Dunkard animal was generically identical with *Diplocaulus* of Texas, it appears that we are dealing, in the genus *Diploceraspis*, with a long-horned form which evolved locally in parallel fashion. A striking novelty in the Dunkard is the relatively enormous snake-like water-dweller *Megamolgophis*, a form quite unknown in the western Redbeds.

A still more marked contrast between the Dunkard and the Wichita lies in the nature of the known reptilian fauna. In Texas, perhaps 50 per cent of all material collected is reptilian — principally remains of cotylosaurs and pelycosaurs. In the Texas fauna, *Edaphosaurus* is a rare animal, apart from two bog deposits which have fortunately yielded a quantity of specimens. In the Dunkard, *Edaphosaurus* is the one relatively common reptile, with identifiable remains reported from some ten localities. Apart from *Edaphosaurus*, reptiles of any sort are rare indeed. They include only the little Blacksville cotylosaur *Melanothyris*, the half skeleton of *Limnosceloides*, the jaw fragment doubtfully assigned to *Baldwinonius* and a very few further scraps — none directly comparable with Texas forms. Captorhinomorph cotylosaurs are rare, diadectids unknown; ophiacodont pelycosaurs are represented only by fragments, edaphosauroids other than *Edaphosaurus* are absent. Most notably, there is no positive indication of the presence of *Dimetrodon* or any member of this sphenacodont group of carnivorous pelycosaurs, which form one of the commonest elements in the Texas fauna (and that of New Mexico as well).

To what are these differences due? In part they may be accounted for by the reasonable assumption that we are dealing with two distinct land areas; connections between them may have been indirect and tenuous or may have been completely interrupted for some modest period of geologic time. On such grounds we perhaps may account for the absence of the embolomeres in the Dunkard, the presence of different types of diplocaulids and the finding in the Dunkard of a few forms, such as *Melanothyris*, *Limnosceloides* and, especially, *Megamolgophis*, which are quite unknown in the abundant Texas material.

It is, however, probable that a great part of the faunal differences

between the two areas may be attributed to differences in the environments in which the two faunas lived. Of the prominent Texas groups, absent or poorly represented in the Dunkard, *Archeria* was essentially aquatic, ophiacodonts in part amphibious, but the other absentees were terrestrial in nature, or mainly so. The missing dissorophids appear to have been the most terrestrial of amphibians. *Eryops*, present in the Dunkard as well as Texas, was a partially terrestrial amphibian type with rather well-developed limbs; but of all Dunkard amphibian citations, 60 per cent are of purely aquatic types — *Diploceraspis* and the lysorophid group—which were quite incapable of venturing onto the land. The most notable Dunkard amphibian type not known from Texas is of this sort — the giant lysorophid *Megamolgophis*. Reptiles, we have noted, are for the most part extremely rare in the Dunkard; and the early reptiles were in general terrestrial types. I have elsewhere (Romer and Price 1940: 175-176) commented on the habits of *Edaphosaurus*, the one reptile well represented in the Dunkard. It appears to have been a plant-eater which fed on lush swamp plants and hence is much more likely to be found in swamp or bog deposits than in beds which, although fluvial in origin, lay adjacent to areas of dry land.

The conclusion to which the discussion above leads us is an obvious one — that the conditions of deposition in the Dunkard area were much more favorable to the preservation of aquatic (in contrast to terrestrial) tetrapods than was the case in Texas; from which may not unreasonably be drawn the further conclusion that the Dunkard area was one of which the living inhabitants were predominantly aquatic or amphibious in nature.

These conclusions from the fossil vertebrate material appear to be in agreement with other evidence. The Wichita beds of Texas are of fluvial and presumably deltaic origin and contain numerous aquatic animals. But plants — mainly xerophytic — and sediments alike suggest that, on the whole, the region was not swampy in nature, but included much dry land — and rather dry, dry land, at that. One can envisage a situation perhaps comparable to the deltas of such rivers as the Tigris-Euphrates system or the Indus, where conditions favorable to aquatic and amphibious forms are present in the immediate neighborhood of the stream channels, but where dry land areas suitable for purely terrestrial forms are close at hand.

Quite different, apparently, is the Dunkard situation. Earlier, the

region had been one with a cyclic repetition of coal swamps and flooding by marine waters. Above the Conemaugh, marine limestones disappear, to be replaced by limestones of freshwater origin, but conditions appear to have been little changed. Cyclic recurrences of coal beds continue throughout most of the Dunkard series and there is little development of redbeds. The plants, of the Washington group, at least, show little change from the presumably lush flora of the late Pennsylvanian. The general impression of the Dunkard area gained from nonvertebrate evidence is thus that of a flat, well-watered coastal region with abundant swamps and lagoons; a region ecologically ideal for an abundant fauna of freshwater fishes and aquatic or swamp-dwelling tetrapods, but with relatively few dry land areas in which the more purely terrestrial types of amphibians and reptiles could flourish in any numbers. The outer part of the Mississippi delta today presents a comparable situation.

This conclusion is in keeping with the nature of the animals noted as making up the Dunkard faunal list: an abundance of fishes, reasonably considered as inhabitants of the streams and lagoons of such an area, including predaceous pleuracanth sharks, lungfishes, palaeoniscoids and — rarer in numbers — crossopterygians and acanthodians; purely aquatic pool-dwelling amphibians such as the “horned” *Diploceraspis* and the lysorophids; a more limited number of rhachitomes of amphibious habits, including *Eryops* and one or more obscure smaller types; of reptiles, an abundance of edaphosaurs which presumably fed on lush swamp vegetation, but few remains of other sorts. The Dunkard facies of the early Permian fauna is thus markedly different from that presented in the southwestern Redbeds. Were we, however, able to get a glimpse of the fauna a bit farther to the east toward the mountains from which the Dunkard sediments came, we might well find a Permian tetrapod assemblage much more comparable with that recorded from Texas or New Mexico.

Pennsylvanian-Permian transition. As has been said, the area here discussed gives us the one opportunity present in North America of obtaining a continuous record of continental vertebrate life from the typical Pennsylvanian coal swamps on into the Permian. The materials collected by the Carnegie Museum parties enable us to make a beginning toward the study of this record. Unfortunately, however, almost nothing was found in the Monongahela group, with which the Pennsylvanian system terminates, and the Conemaugh materials, mainly from the Soho quarry (locality 1), are mostly of fragmentary

nature. We have a tantalizing glimpse of the nature of the transitional faunas; little more. The freshwater fish faunas appear to continue onward from Pennsylvanian to Permian without any appreciable break, although more adequate knowledge would probably indicate changes of specific and quite possibly generic nature among "pleuracanth," lungfishes and crossopterygians and presumably changes of greater magnitude (although no doubt gradual in nature) in the poorly known palaeoniscoid fauna. The known amphibian material is in great measure obscure in nature, but there are two points which stand out: (1) the presence, in *Glaukerpeton*, of an early forerunner of the typically Permian eryopsid group of rhachitomes, and (2) indications (in the form of fragmentary remains) of the rapid development of a long-horned nectridian from an Allegheny predecessor of less spectacular type. Undoubtedly the radiation of primitive reptilian groups was well under way in Conemaugh times, but the known material gives but two isolated facts: that primitive diadectid cotylosaurs, antecedent to those of the Permian, were already in existence (*Desmatodon* and a fragment from Soho); and that (in confirmation of an earlier report from Europe) the specialized pelycosaur *Edaphosaurus* had already evolved.

Although these few data are of interest, it must be admitted that the knowledge of vertebrate evolution gained so far from the Conemaugh is tantalizingly small. But the finds already made give us the hope of future discoveries to broaden the picture of an important transitional stage in tetrapod evolution.

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EXPLANATION OF PLATE I

- FIG. 1. *Sagenodus* cf. *periprion*, pterygoid tooth plate. No. 8501. $\times 1$.
FIG. 2. The same, mandibular tooth plate. No. 8502. $\times 1$.
FIG. 3. *Desmatodon hollandi*, teeth of holotype in crown view, about twice natural size.
FIG. 4. Teeth of small unnamed diadectid from the Conemaugh formation. No. 8567. $\times 2$.
FIG. 5. Parasphenoid of small amphibian. No. 8530. $\times 1$.
FIG. 6. Problematical impression showing *Diploceraspis*-like sculpture. No. 8547. $\times 1$.
FIG. 7. *Lysorophus minutus*, holotype. No. 8564. $\times 1$.
FIG. 8. "Horn" of *Diploceraspis burkei*. No. 8552. $\times 1$.



1



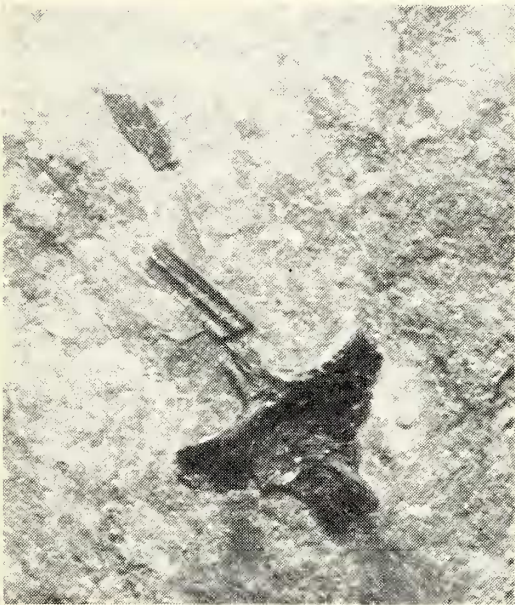
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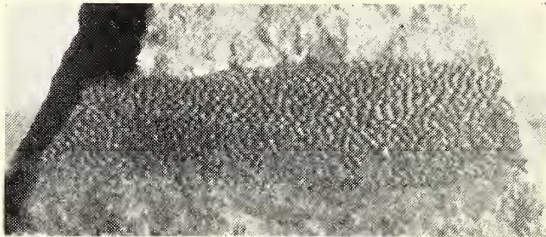
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